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AGRICULTURAL RESEARCH ADMINISTRATION
BUREAU OF ENTOMOLOGY AND PLANT QUARANTINE

Project

Date October 6, 1950 Author Daniel M. Benjamin

SUBJECT—

TITLE

FINAL REPORT

BIOLOGICAL AND ECOLOGICAL STUDIES OF THE RED-HEADED PINE SAWFLY, NEODIPRION LECONTEI (FITCH) AND NOTES ON ITS CONTROL

Forest Insect Laboratory
Milwaukee, Wisconsin

INDEX NO.—

U. S. GOVERNMENT PRINTING OFFICE 16—47272-1

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By

Daniel M. Benjamin

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TABLE OF CONTENTS

	Page No.
INTRODUCTION	1
ACKNOWLEDGMENTS	2
GEOGRAPHIC DISTRIBUTION	3
RED-HEADED PINE SAWFLY OUTBREAKS IN EASTERN NORTH AMERICA	4
HOST LIST AND HOST PREFERENCE	5
SYNONOMY	11
DESCRIPTION OF LIFE STAGES	12
Adult Stages	12
Larval Stages	12
Cocoon Stage	13
Egg Stage	13
LIFE HISTORY AND BIOLOGY	13
Fecundity and Size of Egg Batch	15
Mating	17
Oviposition	20
Egg Stage	21
Larval Activity	22
Parthenogenetic Reproduction and Sex Ratio	41
NATURAL CONTROL FACTORS	42
Egg Parasitism	43
Larval Parasitism	51
Climatic Factors	58
ECOLOGICAL INVESTIGATIONS	58
Introduction	58
High Population Investigations	59
Infestation vs. Defoliation	59
Infestation vs. Number of Colonies per Tree	61
Number of Colonies per Tree vs. Defoliation	62
Site Preference	63
Low Population Investigations (Population Reservoirs)	69
Shawnee National Forest	69
Manistee National Forest	70
Other National Forests Visited	70
Host-Site Susceptibility	71
Meteorological Influences	72
Host Survival	75
POPULATION SURVEY METHODS	81
Survey Criteria	81
Population Survey Procedures	84
ECONOMICS OF RED-HEADED PINE SAWFLY CONTROL	86

TABLE OF CONTENTS (Cont.)

	Page No.
CONTROL PRACTICES	87
Insecticides	87
Equipment	88
Summary of Control Costs	88
Silvicultural Control	91
SUMMARY	92
LITERATURE CITED	97

INTRODUCTION

The red-headed pine sawfly, Neodiprion lecontei (Fitch), is considered by foresters and forest entomologists to be one of the most important native forest insects defoliating young pines in the eastern half of the United States and Canada. The larvae of this sawfly confine their attack to pines belonging to the hard pine group. Occasionally, under conditions of food scarcity, the larvae may migrate to adjacent white pine, tamarack, or deodar cedar to complete their development.

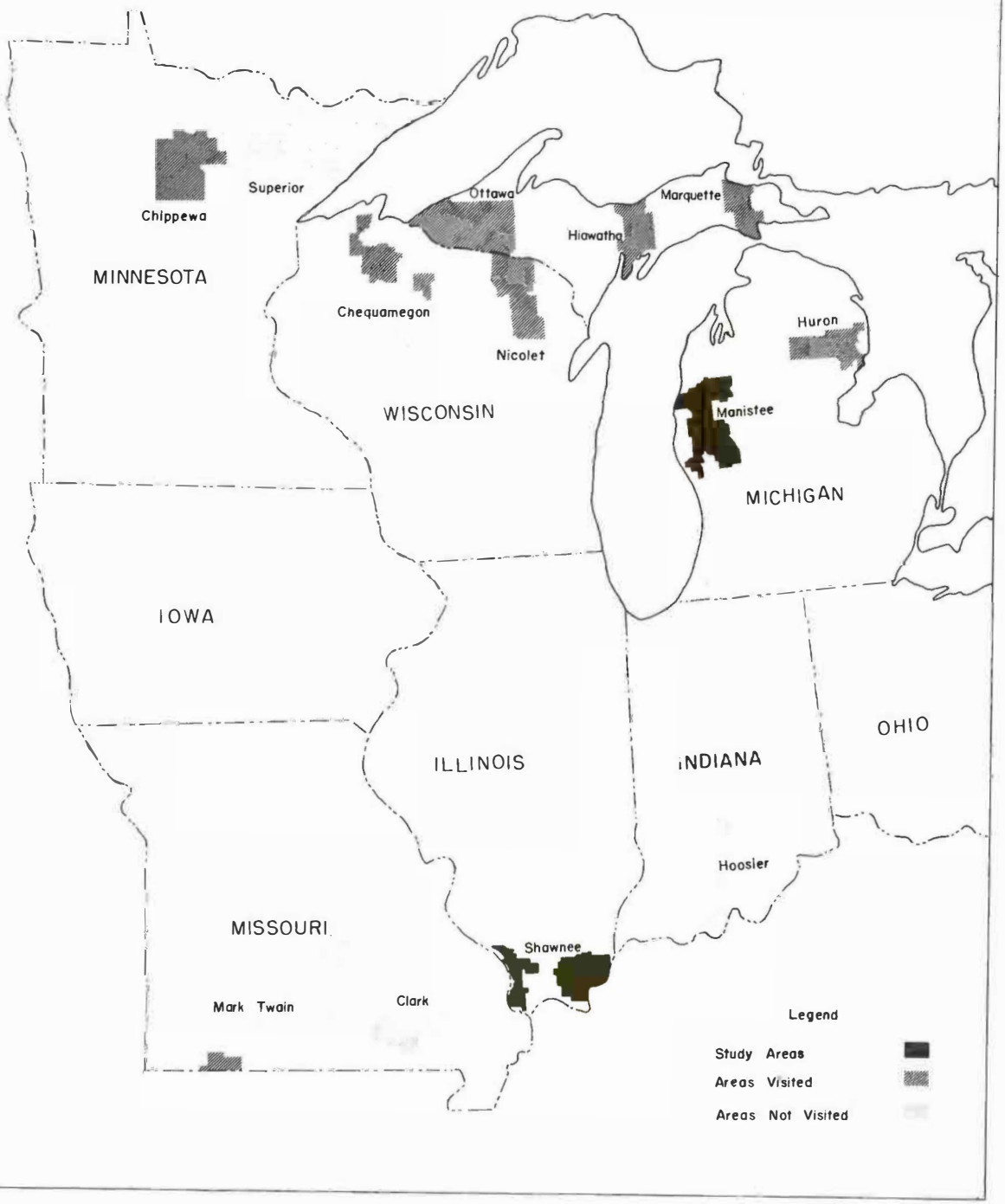
Since its description by Asa Fitch in 1858, the red-headed pine sawfly has been collected in practically every state east from the tier of states bounding the west banks of the Mississippi River to the Atlantic Ocean. In recent years widespread sawfly outbreaks in many of the northern states have resulted in the death or deformity of thousands of acres of young pine plantations. Local sporadic outbreaks of this insect have also killed large numbers of roadside and park pines throughout the entire range of the pest.

In the past, control operations against the red-headed pine sawfly generally have been conducted from the ground, with stomach poisons dispensed by spraying or dusting equipment. Since 1945 control activities on large forest plantation areas have been carried out with highly concentrated organic insecticides dispensed from ground and aerial equipment. With the advent of these powerful insecticides and improved spraying equipment, control of the red-headed pine sawfly over large acreages at relatively low costs is now possible.

Although the red-headed pine sawfly has been a serious pest of pines in eastern North America for several years, few ecological studies on this insect have been conducted. Middleton's biological investigations (1921, 1922) are probably the most complete. Brown and Davisault (1942), Schaffner (1943, 1944, 1945, 1946), Schaffner and Youngs (1946), and Davisault (1949) have also contributed original data to the ecological and biological picture. The literature is opulent, however, with notes concerning the presence, distribution, and small scale control operations. Generally, biological information included in these notes has been obtained from the paper by Middleton.

Because of the current widespread outbreak of the red-headed pine sawfly and the paucity of current factual information concerning its ecology, biology, and control on large forest plantation areas, a research program was initiated to investigate some of the ecological aspects of the sawfly and its control through the application of DDT sprays with aerial equipment. Biological and ecological studies were conducted on the Shawnee National Forest in southern Illinois in 1947, 1948, and 1949 and on the Manistee National Forest in the lower peninsula of Michigan in 1948 and 1949 (Map 1.). Investigations of the control of the red-headed pine sawfly through the application of DDT sprays from aircraft were conducted on the Shawnee National Forest in 1947 and on the Manistee National Forest in 1948. Red-headed pine sawfly infestations on Wisconsin, Minnesota, and Missouri national forests were visited to round out the ecological picture of the sawfly in the North Central region.

MAP 1. NATIONAL FORESTS INCLUDED IN RED-HEADED PINE SAWFLY INVESTIGATIONS.
1947 - 1949



ACKNOWLEDGMENTS

Biological and ecological studies of the red-headed pine sawfly, Neodiprion lecontei (Fitch), and its control through the application of DDT sprays from aircraft were undertaken as a cooperative project between the Division of Forest Insect Investigations of the United States Bureau of Entomology and Plant Quarantine, Region 9 of the United States Forest Service, and the Division of Entomology and Economic Zoology of the University of Minnesota. The biological and ecological investigations were financed by the Milwaukee Forest Insect Laboratory, and the control programs by the United States Forest Service. The Division of Entomology and Economic Zoology of the University of Minnesota acted in an advisory capacity for the biological and ecological studies.

The writer wishes to express his most sincere gratitude to F. C. Craighead, former Chief of the Division of Forest Insect Investigations, for making possible these studies, and to H. A. Hess, former Entomologist in Charge of the Milwaukee Forest Insect Laboratory, for making the original arrangements and for direction and many helpful suggestions during the first year and one-half of the investigations. To C. R. Eaton, Entomologist in Charge of the Milwaukee Forest Insect Laboratory, grateful acknowledgement is given for valuable suggestions and encouragement during the last year and one-half of the studies and for critical examination of the manuscript. The writer wishes to thank his adviser, A. C. Hodson, for suggesting the investigation as a thesis problem, for making the necessary arrangements for the cooperative study, and for helpful advice throughout the project.

Grateful acknowledgement is given for the interest and encouragement of the many members of the United States Forest Service who aided in the study. Particular thanks are due to L. H. Farmer, of the Forest Service, for assistance during the survey and control programs on the Shawnee National Forest in 1947, and to H. C. Fox and R. L. Gallun, temporary employees of the Milwaukee Forest Insect Laboratory, for assistance in the control and ecological studies on the Manistee National Forest in 1948 and 1949. Gratitude is expressed for the assistance rendered by R. C. Marts of the United States Forest Products Laboratory in the preparation and photographing of the shortleaf pine sections.

Sincere appreciation is expressed for the unpublished data made available by many Canadian and American entomologists. In particular, thanks are due the Canadian entomologists A. W. A. Brown and L. Bevisult, and the American entomologist J. V. Schaffner of the New Haven Forest Insect Laboratory, for their unpublished data. The writer wishes to thank C. F. W. Muesebeck and the members of his staff for identifying the parasites and predators of the sawfly and for editing the list of entomophagous insects attacking the sawfly.

GEOGRAPHIC DISTRIBUTION

The red-headed pine sawfly has been collected in practically every state east of the Mississippi River and also from Minnesota, Missouri, Arkansas, Louisiana, and Texas west of the Mississippi. Collections have been made as far south as Manatee County, Florida at approximately 27° north and Jasper County, Texas at 30° north, to as far north as Albanel, Quebec at 49° north and Kindiogami Lake, Ontario at 46° north. Map 2 presents the known distribution of the red-headed pine sawfly in the United States and Canada. The county distribution data included on this map were assembled from the literature, observation in the field, and correspondence with state, federal, and civilian entomologists in the United States and from Canadian entomologists.

It is of interest to observe that although the red-headed pine sawfly has been considered to be native in most states in the eastern half of the United States for several years, collections of the sawfly were not made in Illinois until 1945. The first collections of the sawfly were made in a shortleaf pine plantation south of Bay City, Illinois approximately 60 miles southeast of the "pine hills" on the east banks of the Mississippi. These "hills" contain the only known native hard pine in Illinois, and have never been reported infested with the red-headed pine sawfly during the many insect survey collecting expeditions to the area. The spread of the sawfly into Illinois may possibly have taken place along or through the chain of watershed pine plantations bounding the TVA reservoirs on the Tennessee River. These plantations were heavily infested with red-headed pine sawfly from 1937 through 1941. Planting of shortleaf pine began in 1935 in Illinois, was not greatly increased until 1938, and then reached its peak in 1942.

RED-HEADED PINE SAWFLY OUTBREAKS IN EASTERN NORTH AMERICA

Few comments concerning severe defoliation by the red-headed pine sawfly were published during the nineteenth century. In general, the comments of Fitch (1858), Riley (1867, 1868, 1877), Glover (1868), Norton (1869), Packard (1890), and Dyar (1894, 1895, 1897) referred to defoliation of scattered park and shade pines within some local area and to taxonomic considerations. With the initiation of widespread planting of pure pine stands throughout the eastern half of the United States in the twentieth century, references to both local and widespread damage to pines began to appear more frequently in the literature and in insect pest survey reports. By the middle 1930's severe sawfly outbreaks began to occur in the Lake States, Southern, and Northeastern States. During the late 1930's the sawfly was in general outbreak in Michigan, Alabama, Tennessee, New York, and Vermont. During the 1940's general outbreaks were experienced in Illinois, Wisconsin, Michigan, and New York. The sawfly now is present in outbreak numbers in Wisconsin and lower Michigan. Table 1, a summary of red-headed pine sawfly outbreaks in the United States and Canada, during the past 23 years, indicates the outbreaks which have occurred in practically every region of eastern North America.

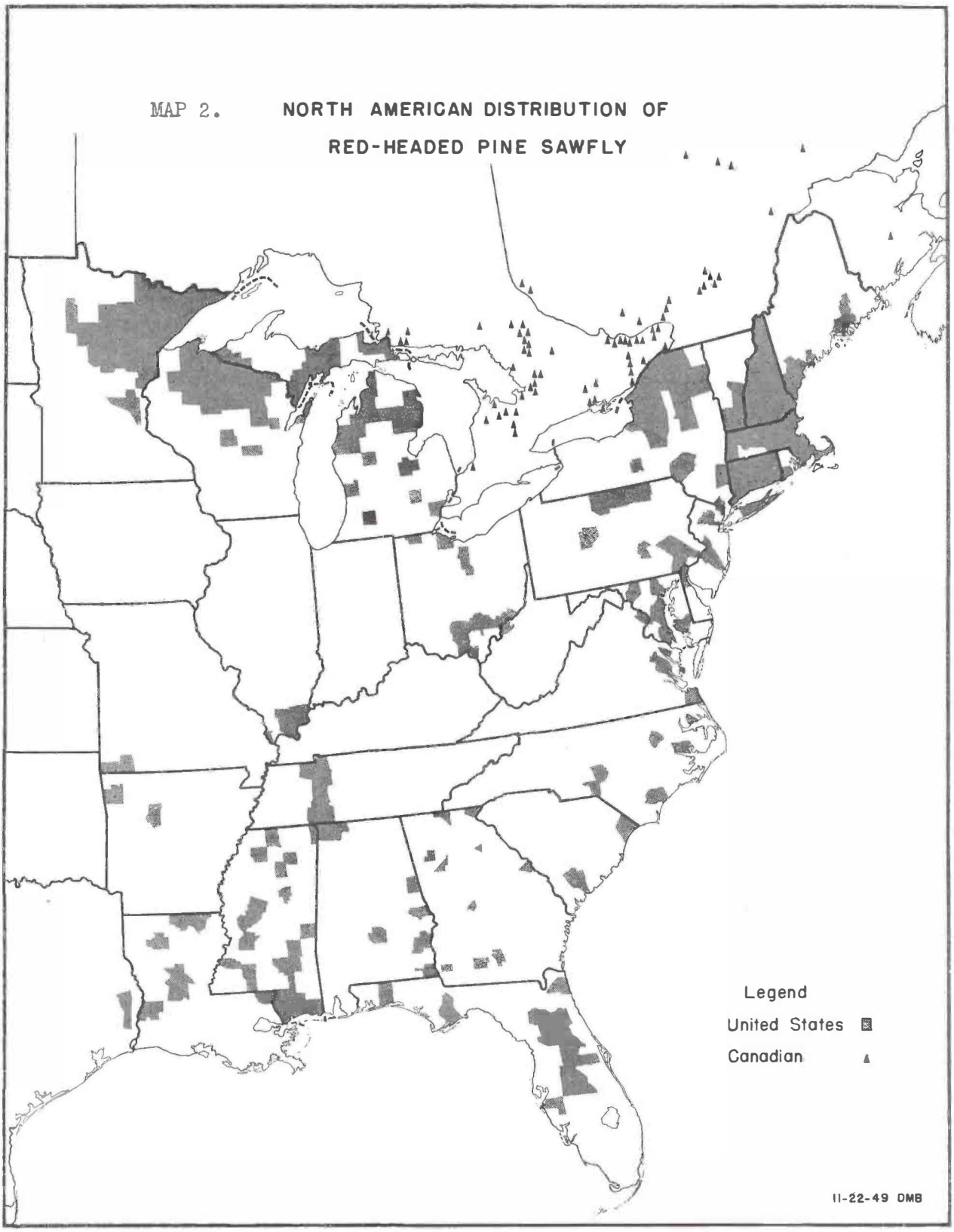

MAP 2. NORTH AMERICAN DISTRIBUTION OF
RED-HEADED PINE SAWFLY
Legend
United States
Canadian
11-22-49 DMB

TABLE 1. RED-HEADED PINE SAWFLY OUTBREAKS IN EASTERN NORTH AMERICA

	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949
1. Lake States																												
Minnesota														? *		*							*	*	*	*	*	*
Wisconsin														*	X	X	X	X	X				*	*	X	X	X	X
Michigan																												
2. Central States																												
Illinois																		*		*				*	X	X	*	*
Missouri																												
Ohio														X	X													
3. Southern States																												
Texas																									*	*		
Florida																												*
Alabama																X	X	X	X	X								
Tennessee																X	X	X	X	X								
4. Atlantic States																												
No. Carolina																		*										
Virginia																			*									
5. Northeastern States																												
New York																X	X	X	X	X	X	X	X	X	X	X		
Connecticut																									X			
Massachusetts						*																						
Vermont																		X	X	X	X							
6. Canada																												
So. Ontario															X			*	*	*		*	*	*	*	*	*	*
No. Ontario															*													
Quebec																*	*	*		*			*					
New Brunswick	X	X	X	X																								

X - Widespread outbreak
* - Local outbreak

HOST LIST AND HOST PREFERENCE

The attack of the red-headed pine sawfly is generally confined to members of the hard pine group. In the eastern half of North America 10 hard pines grow as native species. In addition, several western North American and foreign hard and soft pines have been successfully introduced. Within the range of the sawfly, 16 species of hard pines have been attacked successfully. Sawfly larvae frequently leave completely defoliated hard pines and migrate to nearby pines to continue their feeding. Larvae have also migrated to eastern white pine, western white pine, tamarack, deodar cedar, and Norway spruce under conditions of food shortage and completed their development on these species. Table 2 lists the hard pines, soft pines, and supplemental host species attacked by the red-headed pine sawfly in eastern North America. Common names of species indigenous to North America were obtained from the United States Forest Service Check List (Little 1944).

TABLE 2. LIST OF TREES ATTACKED BY RED-HEADED PINE SAWFLY IN EASTERN NORTH AMERICA

	COMMON NAME	SCIENTIFIC NAME
1.	Jack Pine	*Pinus banksiana Lamb.
2.	Slash Pine	*P. caribaea Morelet
3.	Sand Pine	*P. clausa (Engelm.) Vasey
4.	Lodgepole Pine	P. contorta var. latifolia Engelm.
5.	Japanese Red Pine	P. densiflora Sieb. and Zucc.
6.	Shortleaf Pine	*P. echinata Mill.
7.	Western White Pine	P. monticola Dougl.
8.	Mugho Pine	P. mugo var. mughus
9.	Austrian Pine	P. nigra Arn.
10.	Longleaf Pine	*P. palustris Mill.
11.	Ponderosa Pine	P. ponderosa Laws.
12.	Red Pine	*P. resinosa Ait.
13.	Pitch Pine	*P. rigida Mill.
14.	Eastern White Pine	P. strobus L.
15.	Scotch Pine	P. sylvestris L.
16.	Loblolly Pine	*P. taeda L.
17.	Japanese Black Pine	P. thunbergii Parl.
18.	Virginia Pine	*P. virginiana Mill.
19.	Deodar Cedar	Cedrus deodara (Roxb.) Loud.
20.	Tamarack	Larix laricina (DuRoi) K. Koch
21.	Norway Spruce ?	Picea abies (L.) Karst.

* Hard pines indigenous to Eastern North America

Eggs laid on the foregoing supplementary host species seldom hatch. Eggs laid on northern white pine in southern Illinois did not hatch; mortality in this instance was due to desiccation as the pine needles dried and dropped prior to egg hatch.

From this wide array of host plants growing under vastly varying ecological conditions one might expect a marked preference or selection of certain host species by the ovipositing female sawflies. The lack of detailed information concerning host preference in the various regions of the range of this sawfly prevents critical analysis of the red-headed pine sawfly host preference. Limited published information does, however, indicate certain general conclusions concerning species of pine selected as preferred hosts in most regions of the United States and Canada.

In the Lake States of Minnesota, Michigan, and Wisconsin, where jack pine and red pine grow as native species, jack pine is the preferred host. Red pine is also attacked, but to a lesser degree. Other species of hard pines and adjacent supplemental hosts may be attacked by migrating larvae. The jack pine preference was particularly evident in mixed roadside plantings. Jack pines were reported by Hodson and Christiansen (1945) in Minnesota to be completely defoliated by the sawfly before adjacent red pines were attacked. Similar observations were made by the writer during the past three seasons in Wisconsin and Michigan. This preference was also observed where single jack pine seedlings were accidentally planted within solid blocks of red pine. These stray jack pines were generally attacked and defoliated before the surrounding red pines suffered their initial attack.

The preference for jack pine was observed on a colony per tree basis under epidemic conditions in a mixed planting of red and jack pine on the Manistee National Forest. Table 3 presents a summary of the differential preference for jack pine over red pine by the red-headed pine sawfly on a 1/5th-acre plot where a solid jack pine planting met a solid red pine planting. No insecticidal control applications had been made to this tract.

TABLE 3. DIFFERENTIAL PREFERENCE BY THE RED-HEADED PINE SAWFLY FOR JACK PINE OVER RED PINE ON THE HARISTEE NATIONAL FOREST. 1947 - 1948

	RED PINE			JACK PINE		
	Row 3	Row 2	Row 1	Row 1	Row 2	Row 3
Trees attacked in 1947 - 1948	6	9	7	12	11	9
Trees unattacked in 1947 - 1948	7	4	5	0	1	1
Total number of trees	13	13	12	12	12	10
Total number of colonies - 1948	0	6	6	78	20	19
Number of trees attacked - 1948	0	5	4	12	10	7
Average colonies per tree - 1948	0	1.2	1.5	6.5	2.0	2.7

Over a two-year period 32 of the 34 jack pines were attacked as compared to 22 of the 36 red pines. In 1948, 29 of the 34 jack pines were attacked as compared to 9 of the red pines. On a colony basis, the first, second, and third rows of jack pine averaged 6.5, 2.0, and 2.7 per tree as compared to 1.5, 1.2, and 0.0 per red pine.

Southern Illinois investigations, conducted in 1947 and 1948, indicated that shortleaf pine was by far the preferred host of the sawfly. Seldom was any other species of pine attacked when shortleaf pine was present in the plantation. In the absence of shortleaf pine, pitch pine, loblolly pine, Virginia pine, and red pine was attacked. A striking illustration of this strong shortleaf pine preference was observed in a reservoir planting at Glendale, Illinois. Outbreak populations of the sawfly severely defoliated a poor site shortleaf planting but failed to attack a pitch pine clump growing within the plantation. Figure 1, a photograph of this reservoir planting, shows in the foreground the group of unattacked pitch pine.

Host preference data for the other regions of the United States and Canada, summarized in Table 4, were assembled from the literature and from correspondence with United States and Canadian entomologists. Throughout the Northern States, jack pine was by far the preferred host. Red pine closely approached jack pine in its attractiveness to ovipositing sawfly adults in the New England States. In the Southern States the sawfly exhibited a marked preference for shortleaf pine throughout the range

FIGURE 1. NON-INFESTED PITCH PINE GROUP IN HEAVILY INFESTED SHORTLEAF PINE PLANTATION. GLENDALE, ILLINOIS - 1947.

of this host species. Below the southern range of shortleaf pine, loblolly, slash, and longleaf appeared to be the preferred host. In all regions of the United States the sawfly attacked whatever species of hard pine was available in the absence of its preferred host.

In Ontario and Quebec, Canada, Atwood and Peck (1943), Davisult (1949), and others stated that red pine was the preferred host of the sawfly. Jack, mugho, and Scotch pine were also severely defoliated, but to a lesser degree. White pine and tamarack have been observed under attack of migrating larvae, as mentioned previously.

TABLE 1. LIST OF PINES PREFERRED BY RED-HEADED PINE SAWFLY IN EASTERN NORTH AMERICA

Region	Preferred Host	Secondary Host	Observer
I. Lake States			
A. Minnesota	Jack	Scotch Red	*Hodson
	Jack	Red	Eyer and Zehngraph (1928)
B. Wisconsin	Jack Red		*Benjamin
C. Michigan (Lower)	Jack Red	Scotch	*Benjamin
(Upper)	Jack Red		
		Austrian Scotch Red Jack Mugho	McDaniel (1938)
II. Central States			
A. Illinois	Shortleaf Pitch	Virginia Loblolly Jack Red	*Benjamin
B. Missouri	Shortleaf		*Benjamin *MacAloney
C. Arkansas	Mugho		*Baerg
D. Ohio	Shortleaf	Loblolly Eastern White Lodgepole Jack Austrian	*Folivka Folivka (1938)
III. Southern States			
A. Texas	Loblolly	Shortleaf	*Anderson
B. Louisiana	Longleaf Slash Loblolly	Shortleaf Loblolly	*Kowal *McCrory
C. Mississippi	Longleaf Slash Slash	Shortleaf Loblolly Norway Spruce? Deodar Cedar	*Kowal *Lyle

TABLE 4. (Continued)

Region	Preferred Host	Secondary Host	Observer
IV. Southeastern States			
A. Alabama	Longleaf	Shortleaf	*Kowal
	Slash	Loblolly	
	Slash		*Lund
	Loblolly		
	Shortleaf		
B. Georgia	Longleaf	Shortleaf	*Kowal
	Slash	Loblolly	
	Loblolly		*Lund
C. Tennessee	Loblolly		*Johnston
	Slash		
	Shortleaf	Loblolly	*Zimmerman
		Virginia	
D. Florida	Longleaf	Slash	*Tissot
		Sand	
	Loblolly		*Hetrick
V. Atlantic States			
A. North Carolina	Shortleaf		Beal (1942)
	Loblolly	Spruce ?	*Beal
	Slash	Arbor Vitae?	
		Deodar Cedar	
B. Virginia		Loblolly	*Schoene
		Slash	
		Longleaf	
VI. Northeastern States			
A. New York	Red	Pitch, Jap-	*MacAndrews
	Jack	anese, Black,	
		Scotch, Jap-	
		anese Red,	
		Mughe, White	
		Austrian, Pon-	*Schaffner
		derosa, Larch,	
		Lodgepole	
B. Pennsylvania		E. White, Mughe,	Will (1944)
		Scotch	
C. New Jersey	Mughe	Pitch	*Girth
			Boyd (1945)
D. Connecticut		White, Pitch	Britton and Zappe
		Jack, Scotch,	(1927)
		Mughe, Austrian	

TABLE 4. (Continued)

Region	Preferred Host	Secondary Host	Observer
VII. Canada			
A. Quebec	Red	Jack	*Laviolt Atwood and Peck (1943)
B. Ontario	Red	Jack	*Watson Atwood and Peck (1943)

* From correspondence and unpublished records in the files of the Milwaukee Forest Insect Laboratory.

SYNONOMY

The red-headed pine sawfly was described by Asa Fitch (1858) under the name Lophyrus lecontei in his 4th Report on the Noxious Insects of New York. de Dalla Torre (1894) listed this sawfly under the genus Lophyrus. Rohwer (1918), in his revision of the family Diprionidae, erected the genus Neodiprion using as a basis the species Lophyrus lecontei Fitch. Atwood and Peck (1943) presented a taxonomic treatment of the Canadian sawflies of the genus Neodiprion and among their species listed N. lecontei (Fitch). Ross (1949), in an unpublished Hymenopterous check list, also cited the species as N. lecontei (Fitch). The synonomy of the species is as follows:

Lophyrus lecontei Fitch	Fitch, 4th Report on the Noxious Insects of New York, 4:58-59, 1858
Lophyrus lecontei Fitch	de Dalla Torre, Cat. Hymen. 1; 295, 1894
Neodiprion (Neodiprion) lecontei (Fitch) (genotype)	Rohwer, Proc. Ent. Soc. Wash. 20:84, 1918
Neodiprion lecontei (Fitch)	Atwood and Peck, Can. Jour. Res. D. 21:115, 1943
Neodiprion lecontei (Fitch)	Ross, Hymen. Check List (Unpub.), 1949

DESCRIPTION OF LIFE STAGES

The red-headed pine sawfly, as its name suggests, is a sawfly whose larval stages possess an orange-red head capsule. Fitch (1858) described the adults of this sawfly but made only slight mention of the larval characters. Middleton's (1921) detailed descriptions of the individual larval and adult stages and Atwood and Peck's (1943) taxonomic treatment of both adult and late larval instar stages adequately describe the immature and mature stages of the sawfly. No attempt will be made here to repeat these detailed descriptions.

Adult Stages

Essentially, the adult sawfly female is a rather robust sawfly measuring from 6.0 to 9.5 mm. in length (Figure 2). The head and dorsum of the thorax are rufo-ferruginous. The abdomen is black with ventral aspects of the tergites whitish. The legs are ferruginous with part of the femora and bases of the coxae blackish. The wings are vitreous and subhyaline with dark venation. Antennae are 19 jointed and black.

The male sawfly is smaller, measuring from 5.0 to 6.5 mm. in length and is entirely black with 19 jointed antennae.

Larval Stages

The red-headed pine sawfly hatches as a small (2-5 mm. long) larva with a brownish head capsule. As the larvae feed and molt, the length of the body increases, the body becomes spotted, and the head capsule becomes gradually larger and more orange-red. The 4th and 5th instar larvae, the most frequently encountered stages, have a rufo-ferruginous head capsule with black eye spots surrounding the larval eyes (Figure 3). In these stages the thorax and abdomen may be deep yellow to pale whitish yellow and marked as follows:

1. The prothorax and abdomen are immaculate above with a double row of black spots extending from the mesothorax to the 9th abdominal segment.

2. A second row of supra-spiracular black spots extend from the mesothorax to the 9th abdominal segment.

3. A third row of spots on the dorsal aspect of the spiracular area extend from the mesothorax to the 9th abdominal segment.

4. A fourth row of spots are frequently found on the epipleural area on abdominal segments 1 through 8.

5. The black patch on the epiproct is divided by a light median line.

FIGURE 2. ADULT FEMALE RED-HEADED PINE SAWFLY, NEODIPRION LECONTEI (FITCH).

FIGURE 3. LARVAE OF THE RED-HEADED PINE SAWFLY, NEODIPRION LECONTEI (FITCH).

Cocoon Stage

The cocoon of the red-headed pine sawfly is a tough, single walled, papery, red-brown cylinder with rounded ends. The external surface is dark brown in field specimens and in well fed, reared specimens. The surface is light tan to whitish gray in starved or underfed specimens. Female cocoons are larger than the male cocoons (Figure 4). Middleton (1921) reported that female cocoons averaged 10.3 mm. in length and varied from 9.5 to 11.0 mm. The diameter averaged 4.6 mm. and ranged from 4.5 to 5.0 mm. The male cocoon averaged 7.5 mm. in length with a range of 7.0 to 7.8 mm. and averaged 3.4 mm. in diameter with a range of 3.2 to 3.5 mm.

Egg Stage

The eggs of the red-headed pine sawfly are oval in shape with a very thin, whitish, smooth, shining, translucent shell. They are, according to Middleton (1921), 0.50 mm. long and 0.25 mm. in width. The eggs are laid by the female sawfly in a row of slits cut in the edge of the needles (Figure 5). The shoe-shaped egg pockets are made rather close together, separated from each other by approximately one-third to one-half of their length. All of the eggs generally are laid in a single cluster of needles on a single twig.

LIFE HISTORY AND BIOLOGY

The details of the life cycle and biology of the red-headed pine sawfly have been carefully investigated by Middleton (1921), at East Falls Church, Virginia, by Schaffner (1946) in New York, and by Atwood and Peck (1943) and Davisault (1947, 1949) in Ontario and Quebec, Canada, respectively. As has been mentioned previously, the majority of the references in the literature cite the paper by Middleton; the papers by Schaffner (1946) and Davisault (1949) not having been published.

The general life cycle of the red-headed pine sawfly is as follows: the sawfly overwinters in the prepupal stage incased in a papery cocoon spun in the litter or soil beneath the infested trees. With the onset of warm spring weather development is resumed. Pupation and emergence of the adult sawflies follows in a few weeks. Mating takes place soon after emergence and the female sawflies begin to oviposit a short time later. The eggs, laid individually in a series of slit-like pockets cut in the edge of the pine needles, hatch after approximately three weeks, depending upon the temperature of the particular region. Five feeding and one non-feeding instars are passed through prior to spinning of the cocoon.

In Canada and in the northern part of the United States a single generation of sawflies per year is the rule. In New York and lower Michigan the sawfly completes one generation; a few second generation adults may also emerge. Middleton (1921) reported two generations at East Falls Church, Virginia and mentioned a rather complex life cycle in which the life of a single colony, the "colony period" varied from 12 to 14 months depending on the time of egg deposition. Two generations of the sawfly were also reported by Poliwka (1938) in Ohio. During

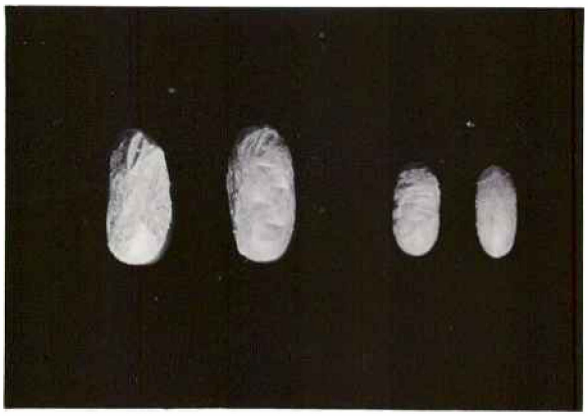


FIGURE 4. COCCOONS OF THE RED-HEADED PINE SAWFLY. FEMALE COCOONS ON LEFT, MALE COCOONS ON RIGHT.

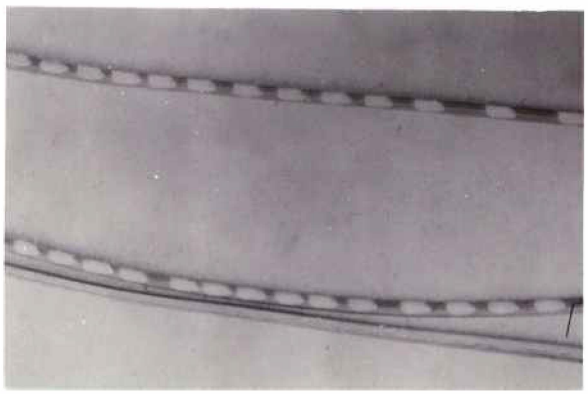


FIGURE 5. EGGS OF THE RED-HEADED PINE SAWFLY.

studies conducted by the writer in southern Illinois in 1947 and 1948 two and a partial third generation per year were encountered. Four to five generations per year were reported in correspondence by Hetrick and Koval in the southeastern part of the United States.

Not all of the sawflies complete their development and emerge as adults during the next adult flight period. Varying periods of diapause have been reported to carry the prepupal sawflies over several years. Daviault (1949) reported diapause up to 5 years in studies conducted from 1938 through 1943 and emphasized that the factors involved in this phenomenon have not been worked out for this insect. Diapause was, in his studies, apparently influenced by the date or lateness of pupation, increasing from 17 percent of the individuals whose cocoons were spun during the first week of August to a high of 77 percent of the individuals whose cocoons were spun in late September. In agreement with these studies, 4.2 percent of the sawfly larvae in the 15 cocoon collections reared by the writer during first generation went into diapause on the Shawnee National Forest in 1947 and 90.4 percent during second generation. Only 1.3 percent of the second generation 1947 sawflies failed to emerge in 1948.

The period during which adult sawflies are active in the field varies throughout the range of this insect. Schaffner and Youngs (1946) reported that although the over-all length of the adult emergence period varied from year to year, the peak of emergence did not vary more than 10 to 16 days. Daviault (1949) summarized the red-headed pine sawfly emergence data in Quebec and also noted that the emergence period was relatively short. He observed that the dates of adult appearance did not vary much from year to year.

Studies conducted by the writer in Illinois indicated that emergence of the first generation began during the first week of May in 1947 and 1948, and reached its peak during the middle of the month. Emergence of the second generation adults began around the middle of July and continued into the first week of August. Third generation adults were first observed around the 15th of September with emergence continuing through the end of October. The diagrammatic sketch presented in Figure 6 illustrates the life cycle of the red-headed pine sawfly in southern Illinois.

Adult emergence of the red-headed pine sawfly on the Manistee National Forest began during the first week of June from 1946 through 1949 according to information supplied by R. W. Blair. The peak was passed during the middle of the month and emergence was completed by the end of June. Figure 7 presents a diagrammatic illustration of the life cycle of the red-headed pine sawfly in lower Michigan.

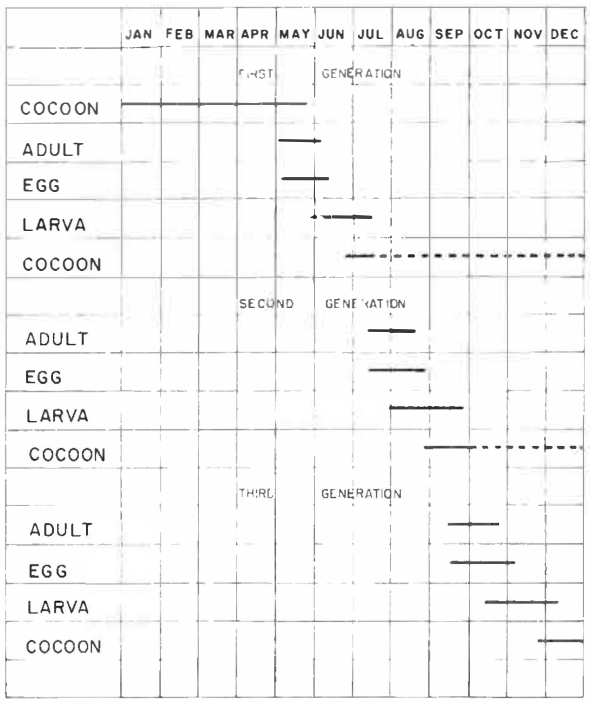


FIGURE 6. DIAGRAMATIC SKETCH OF RED-HEADED PINE SAWFLY LIFE CYCLE IN SOUTHERN ILLINOIS

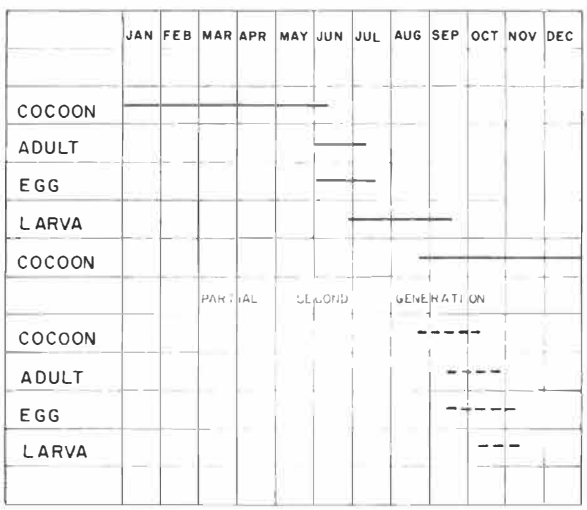


FIGURE 7. DIAGRAMATIC SKETCH OF RED-HEADED PINE SAWFLY LIFE CYCLE IN LOWER MICHIGAN

Fecundity and Size of Egg Batch

Red-headed pine sawfly adult females emerge from their cocoons with their full complement of eggs matured and ready for fertilization. No eggs are matured following emergence from the cocoon. Mating and subsequent oviposition generally begin soon after emergence and egg laying is completed within a short time.

Two approaches may be followed in determining the fecundity of the female sawflies. First, the number of eggs per female may be determined by counting the eggs in the ovaries of the newly emerged females. This count will represent the full egg complement of the female. The second method involves two counts; the number of eggs per batch laid by a caged or wild female added to the number of unlaid eggs remaining in the ovaries of the female. This latter method was used by the writer and found to be the more practical.

Middleton (1921) reported that caged female sawflies laid an average of 82 eggs per batch with a range of 25 to 176. Dissected virgin females had an average of 139 eggs in their ovaries prior to oviposition with a range of 56 to 218. Thus, in his study, an average of 57 eggs were not laid by the female sawflies. Devlault (1949) reported an average of 80 eggs laid per mated female red-headed pine sawfly (with a maximum of 123 eggs) and 95 eggs laid per virgin female (with a maximum of 244 eggs) in cage tests. Southern Illinois studies summarized in Table 5 illustrates the variation in size of field red-headed pine sawfly egg batches on shortleaf, pitch, and jack pines. Eggs per batch averaged from 102 on pitch pine to 141 on jack pine.

TABLE 5. AVERAGE NUMBER OF RED-HEADED PINE SAWFLY EGGS PER OVIPOSITION BATCH COLLECTED ON THE SHAWNEE NATIONAL FOREST 1947-1949

Species of trees	Year	Generation	Total Batches	Total Eggs	Average Number of Eggs per Batch
Shortleaf pine	1947	3	101	13,900	137.6 ± 17.4
	1948	1	86	9,311	108.3 ± 6.7
		2	7	804	114.8 ± 10.6
		3	11	1,481	134.6 ± 6.3
Pitch pine	1947	2	138	14,178	102.7 ± 15.1
		3	2	276	138.0 -
	1948	1	11	1,484	134.9 ± 27.2
		2	1	103	103.0 -
		3			
	1949	2	2	224	112.0 -
		3			
Jack pine	1947	2	10	1,410	141.0 ± 13.3

Sawfly egg collections made on the Manistee National Forest in 1949 averaged 116.5 ± 6.8 eggs per batch on red pine and 108.7 ± 7.6 eggs per batch on jack pine.

Four virgin females laid an average of 137.7 ± 15.8 eggs per batch on shortleaf pine during the third generation in 1947 and 121.3 ± 17.8 eggs per batch during the first generation in 1948.

Twenty-one female sawflies were collected for dissection during the cage and field studies to determine the number of eggs remaining unlaid in their abdomens during 1947 and 1948. An average of 3.04 ± 0.03 eggs remained in the female ovaries after oviposition had been completed. This indicates a more complete egg discharge than the average of 57 unlaid eggs reported by Middleton (1921). Possibly his collections were made prior to the completion of egg deposition. On the Manistee National Forest an average of 2.0 eggs per female were dissected from 5 females after they had completed their oviposition.

Davisult (1949) reported an average of 4.7 eggs per jack pine needle with a maximum of 12 eggs and an average of 8.3 eggs per red pine needle with a maximum of 36 eggs per needle. Atwood and Peck (1943) give the range of eggs per needle on red pine as from 10 to 30 eggs.

Analysis of needle collections on the Shawnee National Forest summarized in Table 6 shows that the red-headed pine sawfly deposited the following number of eggs per needle:

Shortleaf pine	8.7
Pitch pine	11.3
Jack pine	6.3
Virginia pine	5.6

On the Manistee National Forest red-headed pine sawfly eggs per needle averaged 7.5 with a range of 2 to 19 per needle on jack pine and 12.2 with a range of 4 to 35 on red pine.

TABLE 6. AVERAGE NUMBER OF EGGS LAID PER NEEDLE BY THE RED-HEADED PINE SAWFLY

Host Species	No. Egg Batches	No. of Eggs	No. of Needles	No. Eggs per Needle		
				Average	Min.	Max.
(Shawnee National Forest)						
Shortleaf	71	9,065	1,035	8.7	2	31
Pitch	138	14,178	1,246	11.3	1	27
Virginia	4	224	40	5.6	1	10
Jack	10	1,410	222	6.3	2	14
(Manistee National Forest)						
Jack	13	2,065	276	7.5	2	19
Red	13	1,515	139	12.2	4	35

Mating

The premating habits of wild female and male sawflies were difficult to observe because of the dispatch with which the females were mated following their emergence from the ground and because of the small size and agility of the male sawflies. The following statements concerning the premating activities of the red-headed pine sawfly are, therefore, based mainly on observations of reared male and female sawflies liberated in the field both in heavily infested plantations, as well as in plantations where the sawfly population was very low.

Adult sawflies escape from their cocoon by cutting through the end of their cocoon with their mandibles. This operation is performed by thrusting one mandible through the end of the papery cocoon and, while using the other mandible as an extended anchor inside the cocoon, cutting a short slit by bringing the two mandibles together in a pliers-like action. The adult sawfly rotates itself around inside the cocoon as it cuts a circular hole in the end of the cocoon. Escape is made when the hole is of sufficient size to allow the adult to squeeze through. Figure 8 illustrates the emergence holes cut in the end of male and female cocoons. Figure 9 illustrates emergence holes of two common parasites of sawfly.

The female and male sawfly discharge their meconium shortly after emerging from the cocoon - whether this occurs before or after emerging from the ground was not determined.

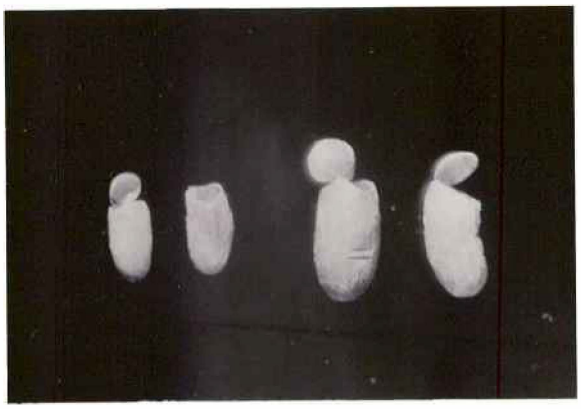


FIGURE 8. COCOONS OF THE RED-HEADED PINE SAWFLY FROM WHICH ADULT SAWFLIES HAVE EMERGED. MALE COCOONS ON LEFT, FEMALE COCOONS ON RIGHT.

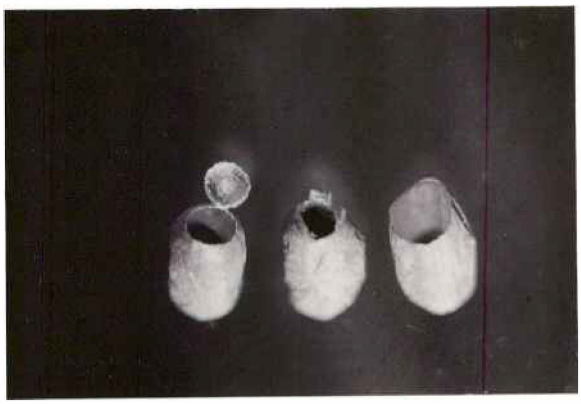


FIGURE 9. COCOONS OF THE RED-HEADED PINE SAWFLY FROM WHICH ADULT LARVAL PARASITES HAVE EMERGED. PHOROCERA HAMATA A. & W. ON LEFT, SPATHIMEIGENIA AURIFRONS TNS. IN CENTER, AND ADULT RED-HEADED PINE SAWFLY ON RIGHT.

Female Activities

Reared females released from stoppered vials in pine plantations where a large population of adult sawflies were active were soon surrounded by male sawflies. Mating generally occurred before the female had walked but a few inches along a pine needle. If the female became agitated by the presence of several excited males, she frequently rejected all of them and took flight; the males generally following her in her flight. When a virgin female sawfly was released in a pine some distance from a heavy sawfly concentration, males were slower to appear. The female walked over several needles, moving from the base to the tip of the needle before returning to the base again to begin inspecting another needle. Finally, when a location to her liking was found, she would walk slowly to the tip of the needle, turn around and take a few steps toward the base of the needle before stopping to take up her presenting position. In this position, with her head toward the base of the needle and her abdomen toward the tip of the needle, she would quietly clean her antennae, legs, and wings while awaiting a mate. If males were not forthcoming, she would wait a few minutes and then change her position to the end of another nearby needle.

Rohwer (1915), in an account of the mating habits of the red-headed pine sawfly, stated that "females of the first generation take as active a part in finding a mate as does the male." This was not the case in southern Illinois studies in 1947 and 1948 during the three adult flight periods. Virgin females remained on a single twig awaiting the appearance of a mate and, except when disturbed by several males attempting to mate with them, they did not stir from this location. Large numbers of male sawflies were attracted to virgin females liberated from sealed vials in heavily infested plantations. Also, large numbers of male sawflies were caught in traps baited with virgin female sawflies and hung in infested plantations (Figure 59). Since no females were observed in the vicinity of the male concentrations around the caged virgin females nor around the male sawflies attracted to the traps during either the first, second, or third generation flight periods, it would appear that the female red-headed pine sawfly takes no active part in seeking out her mate. This does not exclude, however, the role which she obviously plays in attracting male mates.

Male Activities

The male sawfly begins to seek out a mate shortly after emerging from the cocoon. This sex drive is exceedingly strong and males artificially liberated from their cocoons have been observed to begin their search as soon as they were freed. As has been mentioned previously, male sawflies were attracted to the virgin females. In a slight breeze, the males approached the female from the lee side, first alighting on the tree in the vicinity of the female. Darting, arcing flights from twig to twig carried the male closer to the female. In his search the male generally alighted near the base of the needle. After searching a number of needles from their base to their tip and back to the base again, the male flew to another twig and repeated the search. During this time the female remained quiet on her needle - often within view of the male. If two males approached the female at the same time she often buzzed her wings excitedly but made no attempt to capture a mate. In their search, males often encountered other searching males. When this occurred they made several circling flights then darted off to continue their hunt. Encounters on foot were brief with no attempt at combat.

As Rohwer pointed out, no courtship was practiced prior to mating. The female, quietly awaiting her mate, was approached from the anterior by the male, who rapidly crawled over her to complete the copulation.

Mating Habits

Mating was accomplished essentially as described by Rohwer (1915) with the two sawflies facing in opposite directions. The extreme posterior end of the male was bent up at an obtuse angle to meet the truncate abdomen of the female. Rohwer has stated that, "The hypopygideum of the male fits over the knob at the base of the sheath, the (harpes) grasp the sides of the knob in the manner of a ball and socket joint while the position occupied by the (parapenes, sagittae, fossellae) and penis was not observed although they were probably used as in Dhuria macgillvrayi." During copulation the female held her wings flat against her body and spread her legs rather far apart. She moved her antennae up and down slowly and, if disturbed, moved a short distance down the needle, dragging her mate behind her. According to Rohwer (1915) "copulation lasts about 100 seconds." This was not the case in southern

Illinois. Copulation time of 6 matings on the Shawnee National Forest in 1948 averaged 23.6 ± 4.2 minutes, with a range of 10 to 45 minutes.

Post-Mating Habits

Following mating, the male sawfly generally walked around on the needles near the mating site for a few minutes, then took flight. The activities of these males was not followed. Caged males would mate a second time if offered the opportunity within a few days, thus indicating a polygamous tendency in the species. Males who were unable to reach the virgin female left soon after mating began.

Oviposition

Female sawflies began to oviposit within five minutes after mating when confined in a vial with a single pine needle. Under field conditions, oviposition generally began even sooner. Females commonly began searching for suitable oviposition sites immediately following their mating. After a suitable site had been selected (the ecology of the red-headed pine sawfly will be discussed later) the female prepared to select a needle on which to lay her eggs.

Selection of needles in which to oviposit followed a routine pattern in which the female walked from the base of the needle toward its tip while palpating with her antennae. If the needle proved to be unacceptable the female would examine it to its tip and then turn around and return to the twig where she would select another needle. If the needle was acceptable, the female slowly tapped with her antennae until she reached the middle of the needle. At this point she would slowly back down the needle to a point near the base where she would attempt to insert her ovipositor. The female grasped the needle with her fore and mid legs in their normal position and then extended her hind legs well behind her abdomen. Using the scopal pads of her ovipositor as a fulcrum, she pulled down with her legs while pushing forward with her abdomen held in a curved manner. Simultaneous with this bracing, she brought her lancets into play to cut the initial slit into the needle edge. If the spines on the needle did not furnish anchorage and the female slipped, she simply relaxed her grip on the needle and readjusted her position slightly. The initial incision was made slightly in from the edge of the needle on the flat, inner side. The egg pocket itself was cut parallel to the round face of the needle. After the female had made a few cuts with her lancets and the needle appeared to be satisfactory, she relaxed her grip on the needle and withdrew her lancets from the small slit. One step was taken toward the tip of the needle and the female again braced herself as she brought her lancets into cutting action. This time she inserted her lancets to their maximum cutting depth by moving them alternately forward and backward slowly. With the posterior depth attained, the female raised her abdomen and began the forward elongation of the egg pocket. As she cut the slit her lance acted as a guide for the lancets and also kept the lips of the egg pocket spread apart. The egg pocket was enlarged forward to a boot-like shape before cutting ceased. Immediately following the completion of the egg slit the female slowly moved her ovipositor (lance and lancets) back through the egg pocket as she

deposited her egg. The female then lowered her abdomen to contact the needle, folded her ovipositer into place and raised her abdomen before taking a single forward step to begin cutting the next egg slit. Figures 10 and 11 illustrate the oviposition procedure.

When egg laying on a particular needle was completed, the female turned around and walked slowly toward the base of the needle as she cleaned her antennae, wings, and mouthparts. During this period, she also removed the debris accumulated on the needle of her venter during sawing operations. Irregularities in egg spacing on the needles were due to cleaning between pocket sawing activities. Slipping during the initial sawing period was also observed to cause some irregularity.

As has been pointed out in the foregoing discussion, from 1 to 35 eggs were laid per needle depending upon the length of needle available and its acceptability. Acceptance of the second and subsequent needles followed the plan described above. Always an initial cut was made and abandoned before cutting was undertaken for oviposition of the first egg. Why a particular needle becomes unacceptable before a maximum of eggs have been laid in it was not determined. Possibly needle hardness was a factor as female sawflies were frequently observed to abandon a partially completed egg pocket without finishing it or attempting to oviposit.

Needles of the current and previous year were selected and in one instance, a needle bract was used. When the female had exhausted her supply of eggs she walked toward the base of the needle on which she laid her last eggs. The female does not mature additional eggs and has now finished her mission. As if to guard her egg batch, the female remained at the base of the needles in the shelter of the twig until she died or was captured by ants or some other predator (Figure 12).

In regard to the life span of the female and male sawflies, Daviault (1949) observed that 164 females lived an average of 4.5 days with a range of 2 to 17 days while 29 males averaged 3.2 days with a range of 1 to 17 days. No life span determinations were made by the writer. Virgin females were observed, however, to delay oviposition up to five days when they were not fertilized.

Egg Stage

The eggs of the red-headed pine sawfly remain inside the needle during their developmental period. As embryonic development progresses the eggs gradually swell and force the edges of the egg slit apart. Incubation times differ throughout the country, depending greatly on the temperature of the particular region. Daviault (1949) reported incubation averaging 23 to 26 days with a range of 19 to 34 days in Quebec. Middleton (1921) reported that egg incubation periods were closely correlated with temperature. Egg hatch occurred in 21 days when mean temperature averaged 71.23° F. and in 13 days at a mean temperature of 74.59° F., and in 11 days at a mean temperature of 78.80° F. Relative humidity also appeared to have some influence.

FIGURE 10. FEMALE RED-HEADED PINE SAWFLY CUTTING EGG POCKET IN SHORTLEAF PINE NEEDLE PRIOR TO OVIPOSITION.

FIGURE 11. FEMALE RED-HEADED PINE SAWFLY RETURNING SAW THROUGH EGG POCKET AND DEPOSITING EGG.

FIGURE 12. FEMALE RED-HEADED PINE SAWFLY RESTING AT OVIPOSITION SITE FOLLOWING COMPLETION OF EGG LAYING.

Incubation on the Shawnee National Forest averaged 20 days, with a range of 13 to 27 days, during the first generation, 15 days with a range of 13 to 21 days during the second, and 24 days with a range of 21 to 26 days during the third. Eggs laid in November did not hatch.

Larval Activity

The first instar red-headed pine sawfly larvae escape from the egg and needle by wriggling out between the edges of the egg pocket. Practically all larvae from eggs laid on a single needle hatch within a short period of time. The larva from the lowest egg on the needle, that is from the egg laid first by the female, generally hatched first. The other larvae hatch in approximately the order in which the eggs were laid. Often the entire group of larvae from a single needle were observed walking down their host needle following hatching. The head capsule of the first larva was the darkest and the head capsules of the other larvae graded in color progressively from the first larva to the last, which had a practically transparent head capsule.

Five feeding instars and one non-feeding instar are passed through by the red-headed pine sawfly larvae. The duration of these instars varies according to the temperature of the region.

Larval Feeding and Colony Movements

A study of the larval and colony movements was undertaken on the Shawnee National Forest in 1947 to determine when the larvae would be most exposed to aerial sprays. In this study 43 colonies of second generation larvae on 20 open growing shortleaf pines were observed at 2-day intervals.

Shortly after hatching the first instar larvae commenced feeding on the needles from which they hatched or on adjacent needles well back in the dense needle clusters. The larvae chewed small ragged notches in the edges of the needles, generally taking but a few pieces from any one spot on the needle. The progeny of each female fed as a gregarious colony, staying for the most part in the vicinity of the oviposition site in a relatively unexposed location. After the larvae molted, the colony either moved a short distance from the egg site and continued to feed on the lower side of the branch or moved to a sheltered position directly above its egg site. The second instar larvae began to do noticeable damage when several of them assembled around the end of a single needle to feed. These larvae stripped down the edges of the needles, leaving only the central vascular tissue. These central portions soon dried and appeared as reddish, straw-like masses (Figure 13). These straw-like flags served as a useful criterion in making pre-spray population surveys as they were visible from a considerable distance.

FIGURE 13. STRAW-LIKE FLAGS OF SHORTLEAF PINE NEEDLES RESULTING FROM SECOND INSTAR RED-HEADED PINE SAWFLY FEEDING.

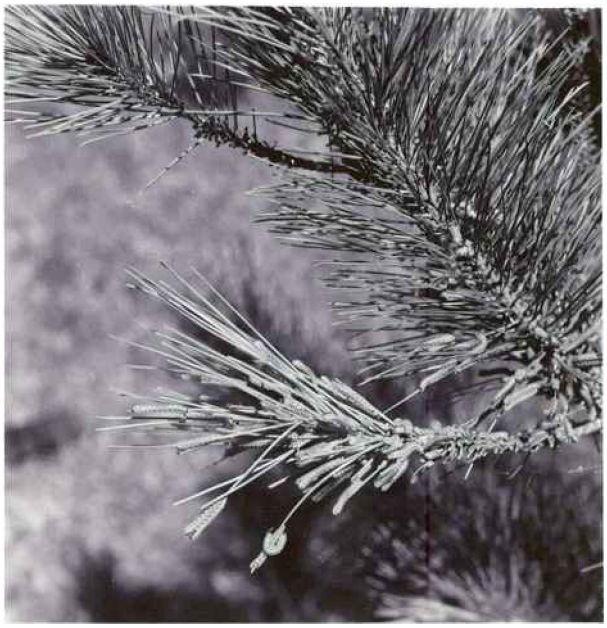


FIGURE 14. COLONY OF RED-HEADED PINE SAWFLY LARVAE FEEDING ON RED PINE.

After molting a second time, the larvae moved out into the open and ascended the tree to feed on the needles of the leader and branch tips. These third instar larvae and subsequent fourth and fifth instars fed voraciously in well exposed positions on the tree. The larvae, often in groups of 3 to 5 per needle, fed as a colony and moved down the leader and branches as they consumed the needles (Figure 3 and 14). After completely defoliating a branch, the larval colonies moved to an undefoliated branch. No apparent pattern was followed in the choice of this next branch. Often a colony would move over several undefoliated branches to select some well exposed distant branch for their feeding site.

When feeding larvae were disturbed, either by the presence of ovipositing parasites or some other factor, they reared back their heads in a characteristic manner, often extended their entire thoracic region several millimeters from the feeding site (Figure 15). If the disturbing factor was close by, the larvae would secrete a droplet of saliva and attempt to flick their heads to deposit the droplet on the intruder. Migrating larvae were often observed to repel attacking ants through the use of this defense mechanism.

Feeding continued during the fifth instar, but gradually decreased in intensity. Frequently the larvae were observed to gnaw cup-shaped holes into the tender bark of the current growth as illustrated in Figure 16. As the individual larvae completed their feeding they spent a short period of inactivity on the tree, then migrated to the ground to spin their cocoon. In sandy soils cocoons were spun in the sand and under leaves and twigs. In heavy soils the larvae migrated varying distances from the tree to spin. This migratory habit and consequent wide-spread distribution of the cocoons has caused much difficulty when seeking the cocoon stage during population analysis studies.

Larval Migration

During ecological studies of high populations of the red-headed pine sawfly conducted on the Manistee National Forest in 1949, an opportunity was available to observe the activity of larvae which had stripped their host tree prior to completion of feeding. In these studies known numbers of second instar larval colonies had been introduced on red pine and jack pine trees to determine the intensity and rate of defoliation. When defoliation of a particular tree neared completion, the surrounding ground and nearby pines were carefully examined for migrating larvae. The ground cover type and the direction and distance from the host tree of all larvae were recorded. For convenience of orientation the study area was plotted to scale. Each tree was located within its particular row by measuring its distance from an established base line. Thus, a tree in row H, twenty-six feet from the base line was referred to as H-26. Trees on which larval colonies were introduced were designated by number and letter referring to the number of colonies introduced and the number of the replicate.

FIGURE 15. RED-HEADED PINE SAWFLY LARVAE REARING BACK WHEN DISTURBED. (LOWER RIGHT AND MID-CENTER).

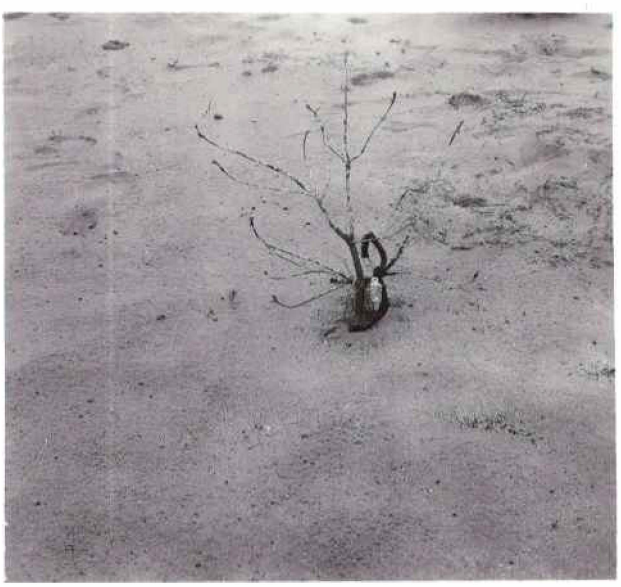


FIGURE 16. HEAVY BARK FEEDING ON JACK PINE CAUSED BY RED-HEADED PINE SAWFLY LARVAE.

Trees having an initial introduced population of 2 larval colonies were thus referred to as 2a, 2b, and 2c respectively.

The selection of comparable trees, both from the standpoint of height as well as gross amounts of total foliage limited somewhat the distribution of the trees. It did not cause any great difficulty in determining the distance of the larval migrants from the initial host tree.

During these studies, larval migration was not observed to begin until complete defoliation was accomplished and much bark was stripped from the tender shoots of the host tree. As was to be expected, trees artificially infested with the largest numbers of colonies were stripped of their foliage earliest and migrations from these trees began first. This sequence of migration also aided in keeping track of a particular tree population.

In the following discussion, larval migration from the defoliated pines will be discussed in a chronological order. That is, migration from those trees first stripped of their foliage will be treated first followed by migration from the later trees. The 4 colony tree attack will be discussed first and followed by the migrations from the 2 and 1 colony trees.

(Sandblow Plantations - Jack Pine)

The first study area on which migration studies were conducted was a 1-foot jack pine sandblow plantation located on a slight southern slope in the plantation illustrated in Figure 17. Figure 19 is a diagram of the portion of the plantation included in these studies. Tree 4-a. Defoliation of tree 4-a, a 4-colony tree, was completed on July 5, and the 3rd and early 4th instar larvae remained on the tree crawling over one another from branch to branch as if in search of additional food. On the day following defoliation, 19 larvae still remained on the host tree. Approximately 170 larvae were observed migrating on the sand at the following distance from the host tree:

Direction	Distance (Inches)	Number of Larvae
N	2	1
NW	18	1
NW	10	18
W	10	65
W	22	1
S	29	9
S	17	75

In addition to these migrants, 23 larvae had established themselves on tree O-18, 3 feet south of their host tree. Two days after defoliation no larvae remained on the host tree. One additional larva had reached tree O-18, bringing the total population to 24 larvae. One larva had reached tree F-19, 7 feet from the host tree. On the bare sand, 168 dead migrant larvae were observed in shallow depressions in the sand at the

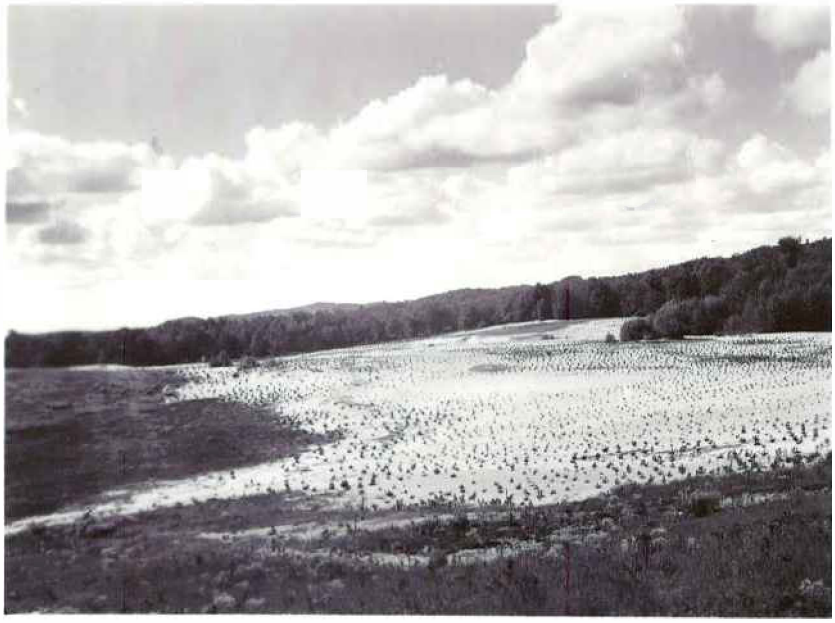


FIGURE 17. ONE-FOOT JACK PINE IN SANDBLOW AREA IN WHICH LARVAL MIGRATION STUDIES WERE MADE.

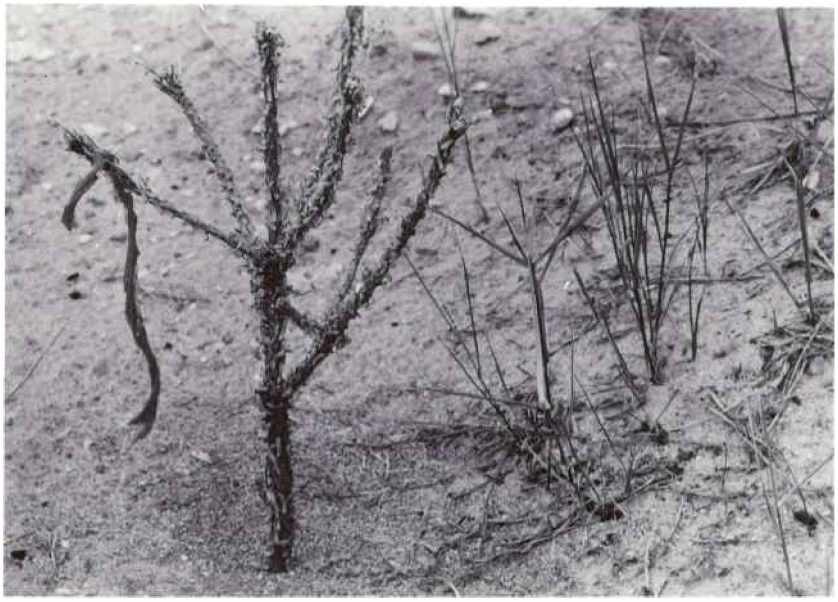


FIGURE 18. RED-HEADED PINE SAWFLY LARVAE MIGRATING FROM DEFOLIATED RED PINE.

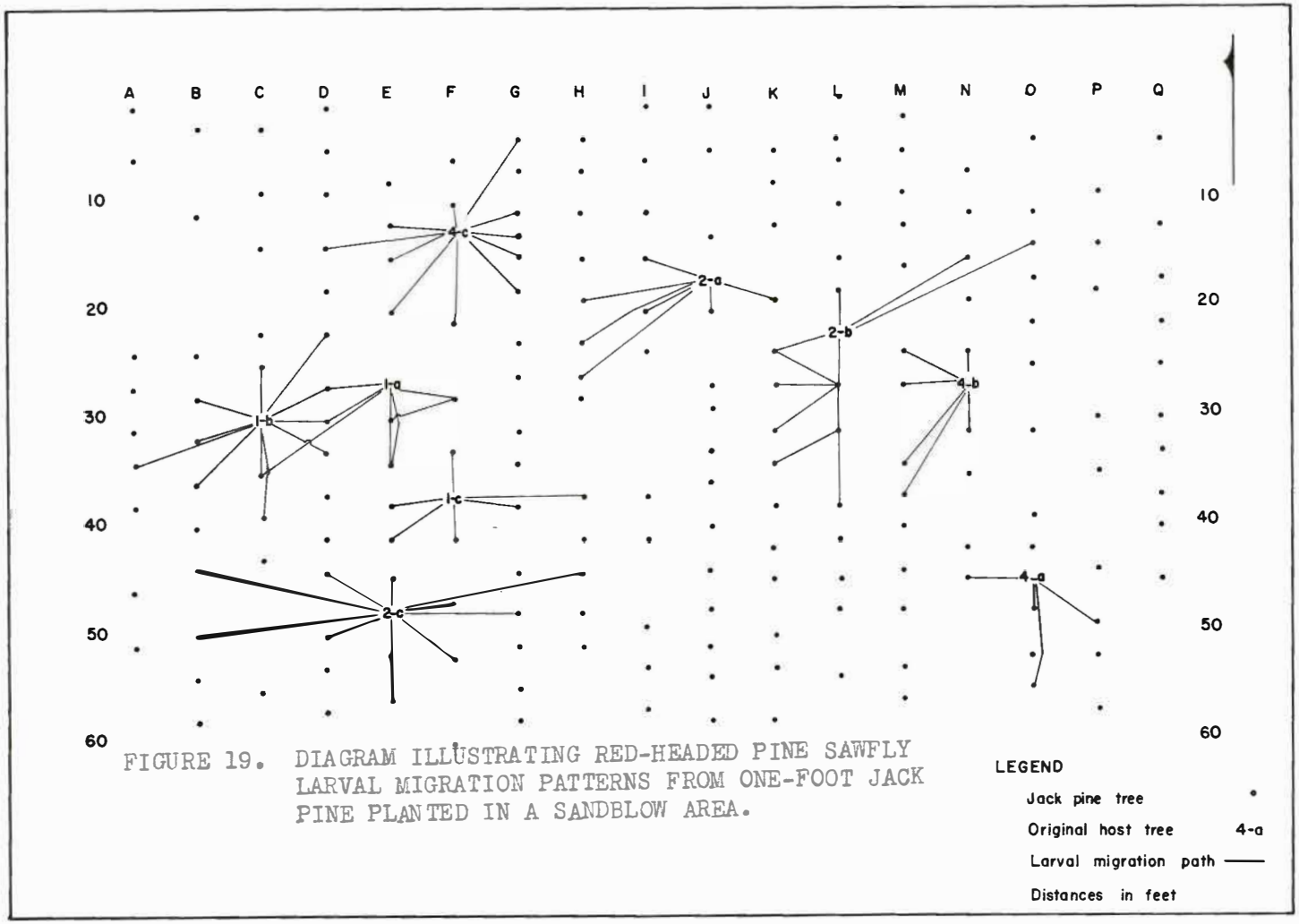


FIGURE 19. DIAGRAM ILLUSTRATING RED-HEADED PINE SAWFLY LARVAL MIGRATION PATTERNS FROM ONE-FOOT JACK PINE PLANTED IN A SANDBLOW AREA.

following distances from the host tree:

Direction	Distance (Inches)	Number of Larvae
N	22	150
E	36	4
W	62	14

These larvae, which had wandered into shallow depressions in the sand, were observed as they succumbed to high sand temperatures when the sun broke through a light cloud cover. On the 5th day, one additional larva was observed on tree O-48 and single larvae on trees O-55 and N-45, 10 feet and 6 feet from the host tree respectively. By the time larval feeding had been completed, 4 trees had been infested by migrating larvae from the host tree. Tree O-48 was 50 percent defoliated by the migrating larvae while the other 3 trees showed minor amounts of larval feeding.

Tree 4-b. On July 5, the day defoliation of tree 4-b was completed, the one larva which left the host tree perished on the bare sand 3 inches east of the host tree. On the day following completion of defoliation, 77 larvae had established themselves on the following surrounding trees:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
N-24	8	7
N-34	8	9
N-37	1	12
N-31	60	4

In addition to these migrants 2 larval colonies were observed on the host tree and 80 larvae on the ground around the host tree as follows:

Direction	Distance (Inches)	Number of Larvae
NW	4	1
E	4	2
W	15	1
S	15	2
SE	23	25
SW	16	48
SW	108	1

Two days after defoliation was completed, most of the larvae had left their host tree. Approximately 40 more larvae had reached tree N-31 to bring the population to about 100 larvae. Four additional larvae had reached tree N-34 and 2 larvae N-24 to bring the population on these trees to 12 and 10 larvae respectively. Three days after defoliation, a few larvae still remained on the host tree. The larvae on tree N-31 had broken into two colonies and were feeding vigorously. On the 10th day 1 larva appeared on tree N-27 and on tree N-24. The origin of these larvae is unknown; possibly they came from tree 2-b. When larval activity

was completed 6 small jack pine trees had been infested by migrating larvae. Only two of these trees escaped serious injury; the others were defoliated as follows:

Host Tree	Percent Defoliation
H-24	25
H-27	25
H-34	-
H-37	50
H-24	-
H-31	75

Tree 4-c. Defoliation of tree 4-c was completed on July 7. No migrating larvae were observed on the ground in the vicinity of the host tree. The majority of the larvae were still on the host tree feeding on the bark and milling over the bare branches. A few migrants had left the host prior to the observation hour and had successfully established themselves on the following trees:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
E-12	2	6
E-15	5	7
D-14	4	12

On the day following defoliation many larvae still remained on the host tree. Migrants were observed on the bare sand at the following distances from the host tree:

Direction	Distance (Inches)	Number of Larvae
S	2	1
SW	12	1
NW	3	1

Four days after defoliation a few larvae remained on the host tree. Larval migrants had successfully established themselves on the following host trees:

Host Tree	Number of Larvae Previous	New	Total	Distance from Host Tree (Feet)
D-14	4	2	6	12
E-12	2	10	12	6
E-15	5	19	24	7
E-20	-	5	5	9
F-10	-	16	16	3
F-21	-	21	21	8
G-11	-	1	1	7
G-18	-	1	1	8

By the eighth day after defoliation, the following larval population increases on the foregoing host trees were observed:

Host Tree	Number of New Larvae	
E-15	2	
E-20	2	
G-11	4	
G-15	3	New host attacked at 6 feet

On the 19th day after defoliation, larvae were beginning to leave their host tree to spin cocoons. The following dead larvae were observed under their host trees:

Host Tree	Number of Dead Larvae
E-15	9
E-20	3
F-10	4
F-21	11

On the 26th day two additional trees were infested by migrating larvae - apparently from this original larval lot. These trees G-4 and G-13 were 11 and 6 feet respectively from the host tree.

Final defoliation injury was observed on 12 trees; the following trees showed measurable defoliation:

Host Tree	Percent Defoliation
D-14	6
E-15	75
E-20	6
F-10	12

Tree 2-a. Two colony tree 2-a was completely stripped of its foliage on July 10. Larval migrants were observed already established on the following adjacent trees although the major number of larvae still remained on the host tree:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
I-20	1	7
I-15	1	7
J-20	1	3
K-19	1	6

Two days later larvae had reached the following trees:

I-20	10 additional larvae
J-20	25 additional larvae

At 19 inches from the host tree, 35 larvae had succumbed in a shallow depression in the sand. By the 5th day 16 additional larvae had reached tree J-20, bringing the total population to 42 larvae. Five dead larval migrants were observed below tree J-20 on the 13th day - these larvae appeared diseased. On the 38th day larval defoliation activity was about completed. Migrant larvae were observed on the following trees - their original host tree probably being tree 2-a:

Host Tree	Number of Larvae
H-19	1
H-23	1
H-26	1

In summary, 7 trees were infested by migrants from tree 2-a. Damage to these hosts was minor, trees I-20 and J-20 suffering approximately 25 percent defoliation.

Tree 2-b. Defoliation of tree 2-b was completed on July 10. No migrants were observed on the ground although the following trees were infested:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
K-24	7	6
L-18	18	4
L-27	½	5

Two days later 3 additional larvae reached tree L-18 and approximately 80 larvae had reached tree L-27 to bring the total larval population to over 100. On the 5th day the original host tree was barren of larvae; the majority of the larvae apparently migrated to trees L-27 and L-18 which now had over 150 and 31 larvae respectively. Tree K-24 received two additional larvae. On the 13th day defoliation of tree L-27 was finished. Twenty larvae still remained on the tree and 50 had migrated to tree L-31. On this day trees K-31 and K-27 were also attacked for the first time by 1 and 5 migrant larvae from tree L-27. Three larvae also reached tree K-24. On the 16th day stripping of tree L-31 was completed; 26 larvae remaining on the tree. Two migrant larvae appeared on tree K-36, 7 feet from the tree L-31 and 17 feet from the original host tree. One larva was observed on tree J-36, 17 feet from the L-31 and 18 feet from the original host tree. On the 23rd day 2 larvae appeared on tree H-15, 16 feet from the host tree, and 1 larva on tree G-14, 20 feet from the host tree.

By the end of the larval activity period 10 trees had been infested by migrant larvae. Four of these trees suffered severe injury as follows:

Host Tree	Percent Defoliation
K-24	50
L-18	50
L-27	100
L-31	100

Tree 2-c. No larval migration was observed on July 11, the day defoliation of tree 2-c was completed. On the day after defoliation, migrants were observed on the following trees:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
B-50	1	18
D-44	1	7
D-50	1	7
E-52	2	4

On the second day 65 additional larvae reached tree E-52. Tree F-52, 7 feet from host tree, was infested by 1 larva. On the 4th day the following increases in larvae were observed:

Host Tree	Number of Larvae
D-44	3
D-50	4
E-52	8
F-47	1 new at 6 feet from host
F-52	1

On the 12th day defoliation of tree E-52 was completed and all larvae had left the tree. Tree E-56 was observed to have 3 larvae and E-45, 3 larvae. By the end of the larval activity period the following three trees had become infested:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
E-44	2	16
G-48	1	17
H-44	1	17

Final infestation included 11 trees, two of which, D-50 and E-52, suffered 3 percent and 100 percent defoliation respectively.

Tree 1-a. On July 7, the day defoliation of tree 1-a was completed, 3 larvae were observed migrating 33 inches west of the host tree on the bare sand. In addition, the following trees were infested with larval migrants:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
F-28	1	7
E-30	1	3
D-30	6	7
D-27	1	6

On the following day, larvae still remained on the host tree. No additional migrant larvae were observed on surrounding trees although 14 larvae were observed on the sand at the following points:

Direction	Distance from Host Tree (Inches)	Number of Larvae
S	44	2
SW	85	8
NW	86	2
N	86	1
NE	98	1

On the fifth day the following nearby trees were infested with larvae:

Host Tree	Number of Larvae	Remarks
E-30	1 (colony)	
D-27	29	Increase of 28 larvae
D-30	37	Increase of 31 larvae
C-35	2	New infestation at 14 feet
F-28	2	Increase of 1 larva
E-34	31	New from tree E-30 at 7 feet

Tree E-30 was completely stripped on the fifth day. The larvae next moved to tree E-34. On the eighth day 2 additional larvae were observed on tree F-28. By the end of the larval activity period 6 trees had been infested, 3 of them suffering severe defoliation as follows:

Host Tree	Percent Defoliation
E-30	100
E-34	50
D-27	25

Tree 1-b. Defoliation of tree 1-b was completed on July 13. On this date many larvae remained on the host tree. Migrant larvae were observed on the following trees:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
E-32	3	7
C-35	9	5

Two days later migrant larvae were observed on the bare sand and on the following trees:

Direction	Distance (Inches)	Number of Larvae
NW	72	1
SW	72	1
S	3	17

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
B-32	5 additional	7
C-35	8 "	5
B-30	55 (37 from tree 1-a)	6
D-33	3	7
D-22	2	10
D-27	38 (29 from tree 1-a)	6

Ten days after defoliation larval migrants were observed on the following trees:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
B-28	1	7
B-32	(5 additional)	7
A-34	1	13
B-36	7	9
C-25	1	5

On the 13th day tree C-39, 9 feet from the host tree, was observed infested with a small colony of larvae.

In the final examination 11 trees were observed to show feeding damage, the following seriously injured:

Host Tree	Percent Defoliation
B-32	12
B-36	3
D-30	93
D-27	85

Tree 1-c. Complete defoliation of tree 1-c was accomplished on July 17. One larval migrant was observed on tree F-33, 4 feet from the host. On the 5th day, 3 migrants were observed on tree F-41, 4 feet from the host, and on the 9th day tree E-38, 7 feet from the host, became infested with 2 larvae. During the next week, the following trees became infested:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
E-41	1	8
C-38	1	6
H-37	1	12

None of the 6 trees infested from the original host tree were seriously injured.

Summary. In the foregoing studies, 21 larval colonies were liberated on 9 trees. After these trees had been stripped of their foliage, the migrating larvae succeeded in reaching 72 nearby trees and establishing themselves. Varying degrees of defoliation injury resulted, depending upon the size of the larval population. Eighteen of the attacked trees sustained defoliation in excess of 25 percent; 4 of the 18 trees were completely stripped. The data show that the larvae readily left their host after completely defoliating it. Distances as great as 19 feet were successfully traversed to reach a new host tree. No apparent time pattern of migration was evident. Migrations were observed at all hours of the day and evening. The larvae did tend to follow each other, as illustrated in Figure 18, and as high as 150 larvae were observed on a single nearby tree after the defoliated host was abandoned. Table 7 summarizes the migration attack and injury sustained.

TABLE 7. ONE-FOOT JACK PINE TREES ATTACKED BY MIGRATING RED-HEADED PINE SAWFLY LARVAE

MANISTEE NATIONAL FOREST - 1949

Host Tree	Attacked Tree	Distance from Host (Feet)	Number of Larvae	Percent Defoliation
4-a	M-45	6	1	-
	O-48	3	25	50
(4 trees)	O-55	10	1	-
	P-49	7	1	-
	Average =	6.5	28	
4-b	M-24	7	10	25
	M-27	?	1	25
(6 trees)	M-34	9	12	-
	M-37	12	1	50
	M-24	?	1	-
	N-11	4	100	75
	Average =	8.0	125	
4-c	D-14	12	6	6
	E-12	6	12	-
	E-15	7	27	75
(11 trees)	E-20	9	7	6
	F-10	3	16	12
	F-21	8	8	-
	G-4	11	1	-
	G-11	7	5	-
	G-13	6	1	-
	G-15	6	3	-
	G-18	8	1	-
	Average =	7.5	87	

Table 7 - (continued)

Host Tree	Attacked Tree	Distance from Host (Feet)	Number of Larvae	Percent Defoliation
2-a	H-19		1	-
	H-23		1	-
(7 trees)	H-26		1	-
	I-15	7	1	-
	I-20	7	11	25
	J-20	3	42	25
	K-19	6	1	-
	Average =	5.7	58	
2-b	J-16	18	1	-
	K-24	6	9	50
	K-27	8	5	-
	K-31	11	1	-
(10 trees)	K-38	17	2	-
	L-18	4	11	50
	L-27	5	150	100
	L-31	9	50	100
	N-15	16	2	-
	O-14	20	1	-
	Average =	11.4	252	
2-c	B-44	18	2	-
	B-50	18	1	-
	D-44	7	4	-
(11 trees)	D-50	6	5	-
	E-45	3	3	-
	E-52	4	75	100
	E-56	8	3	-
	F-47	6	1	-
	F-52	8	2	-
	G-48	12	1	-
	N-44	19	1	-
	Average =	9.7	98	
1-a	C-35	14	2	-
	D-27	6	29	50
	D-30	7	37	-
(6 trees)	E-30	3	1 colony	100
	E-34	7	1 colony	25
	F-28	7	4	
	Average =	7.3		

Table 7 - (continued)

Host Tree	Attacked Tree	Distance from Host (Feet)	Number of Larvae	Percent Defoliation
1-b	A-34	13	1	-
	B-28	7	1	-
(11 trees)	B-32	7	13	12
	B-36	9	7	3
	C-25	5	1	-
	C-35	5	17	-
	C-39	9	1 colony	-
	D-22	10	2	-
	D-27	6	38	25
	D-30	6	55	93
	D-33	7	1	-
	Average =	7.6		
1-c	E-38	7	2	-
	E-41	8	1	-
(6 trees)	F-33	4	1	-
	F-41	4	3	-
	G-38	6	1	-
	H-37	12	1	-
	Average =	6.8	9	

(Sandblow Plantation - Red Pine)

Larval migration activities following defoliation on the one-foot red pine study plots followed, in general, the pattern exhibited by the larvae leaving the one-foot jack pine after defoliation of their host trees. Figure 20 presents the migration pattern and Table 8 lists the trees attacked and their respective distance from the host tree.

Larval migrants successfully traversed distances great as 19 feet to establish themselves on young red pines. The original population of 21 colonies on 9 trees spread out to attack 52 additional trees, seriously defoliating 19 and stripping 10 trees completely. In the case of tree 4-a, two colonies of approximately 150 larvae left the host tree to migrate 6 feet across the small wooded patch to establish themselves on tree H-34. After stripping this tree, the colonies split, one part migrating 5 feet north to strip tree H-29, and the other part migrating 4 feet south to strip tree H-38. After stripping tree H-38, the larvae migrated 8 feet further south to strip tree H-46. Of the 13 trees attacked by the migrating larvae, 5 trees were completely stripped. The larvae which left tree 4-b, attacked 7 trees. Approximately 100 larvae established themselves on tree J-34 which they completely defoliated and then moved on to tree I-36 which they defoliated 93 percent.

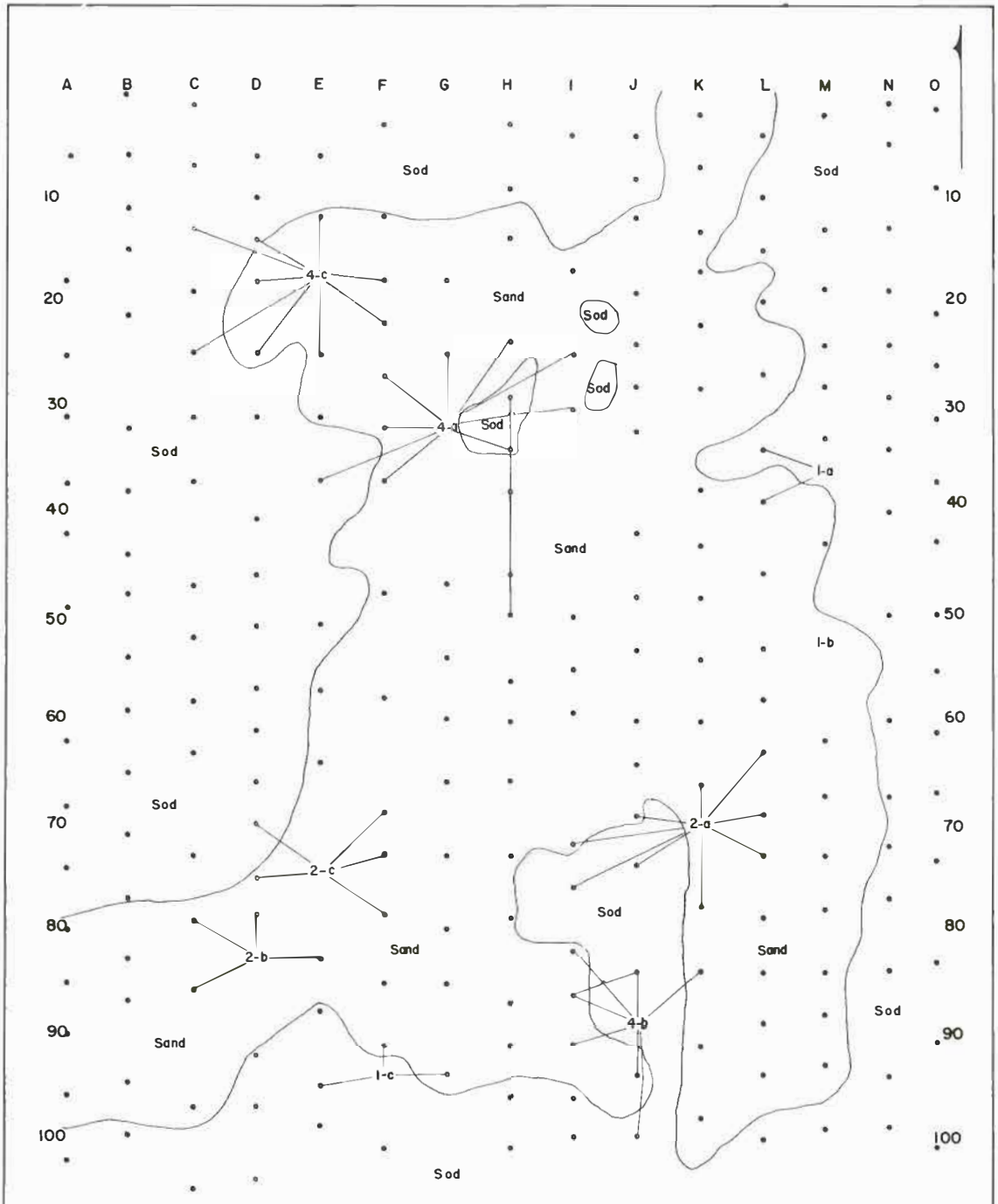


FIGURE 20. DIAGRAM ILLUSTRATING PED-HEADED PINE SAWFLY LARVAL MIGRATION PATTERNS FROM ONE-FOOT JACK PINE PLANTED IN SANDBLOW AREA.

Migrants from tree 4-c established themselves on 9 trees, 4 of which they severely injured; two trees were completely defoliated. Migrants from the 2 colony trees infested 9, 4, and 5 trees up to 13, 7, and 9 feet respectively from the host trees. Seven trees were severely injured.

TABLE 8. ONE-FOOT RED PINE TREES ATTACKED BY MIGRATING RED-HEADED PINE SAWFLY LARVAE

MANISTEE NATIONAL FOREST - 1949

Host Tree	Attacked Tree	Distance from Host (Feet)	Number of Larvae	Percent Defoliation
4-a	E-37	13	1	-
	F-27	8	5	-
	F-32	6	9	3
	F-37	8	5	100
(13 trees)	G-25	7	12	25
	H-24	10	11	93
	H-29	7	60	100
	H-34	6	150	100
	H-38	8	30	100
	H-46	16	1 colony	100
	H-50	19	7	6
	I-25	14	11	12
	I-30	12	10	25
	Average = 10.3			
4-b	I-82	10	1	-
	I-86	7	5	93
(7 trees)	I-91	6	1	-
	J-84	6	100	100
	J-94	4	6	25
	J-100	10	3	-
	K-84	8	4	-
	Average = 7.3		120	
4-c	C-13	13	1	-
	C-25	14	1	-
	D-14	7	6	-
	D-18	6	16	100
(9 trees)	D-25	9	10	75
	E-12	6	6	-
	E-25	7	2 1	99
	F-18	6	10	100
	F-22	7	18	25
	Average = 8.3		69	

Table 8 - (continued)

Host Tree	Attacked Tree	Distance from Host (Feet)	Number of Larvae	Percent Defoliation
2-a	I-72	12	2	-
	I-76	13	11	100
	J-69	6	9	50
	J-74	7	26	-
(9 trees)	K-66	6	14	12
	K-78	8	14	50
	L-63	10	1	-
	L-69	7	4	-
	L-73	7	5	-
		AVERAGE = 8.3	86	
2-b	C-79	7	1	-
	C-86	7	1	-
(4 trees)	D-79	4	4	50
	E-83	6	13	50
		AVERAGE = 6.0	19	
2-c	D-70	8	1	-
	D-75	6	2	100
(5 trees)	F-69	9	2	-
	F-73	6	6	-
	F-79	7	13	25
		AVERAGE = 7.2	24	
1-a	L-34	7	27	25
(2 trees)	L-39	7	18	-
		AVERAGE = 7.0	45	
1-b	-	-	-	-
1-c	E-95	6	34	-
(3 trees)	F-91	4	1 colony	25
	G-94	6	7	-
		AVERAGE = 5.3		

(Sandblow Plantation - Jack Pine - Natural Infestation)

The distance red-headed pine sawfly larvae were able to migrate and establish themselves under field conditions was investigated in the sandblow areas of a 1-foot jack pine plantation under heavy natural attack. In these studies, jack pines in the vicinity of completely defoliated pines were examined for the presence of sawfly larvae as soon as the naturally infested host tree appeared free of larvae.

Tree 360. Figure 21 illustrates the migration pattern from tree 360, after all larvae had left on July 15, 1949. Seventy-six of the larvae survived migration and established themselves on adjacent trees up to 8 feet distance as follows:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
B-15	11	7
B-26	1	8
C-10	10	4
C-18	36	4
C-21	18	7

Tree 359. Figure 22 illustrates migration from tree 359, a nearby naturally infested jack pine sandblow tree. Successful migration of 91 larvae to maximum distances of 10 feet was accomplished as follows:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
B-15	60	6
B-19	1	7
B-24	2	10
C-10	23	6
C-26	1	10
D-16	4	6

Trees 366-374. Figure 23 illustrates the migration from tree 374 across the sandblow. Successful migrations of 59 larvae were made up to a maximum distance of 13 feet as follows:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
B-12	4	11
B-17	3	7
B-22	31	6
C-14	6	7
C-26	10	5
D-21	1	6
E-17	1	13

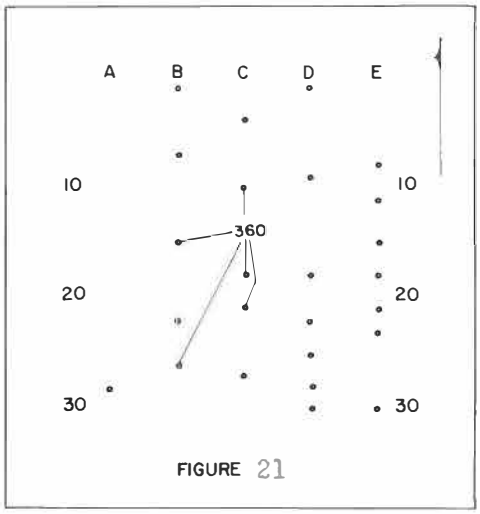


FIGURE 21

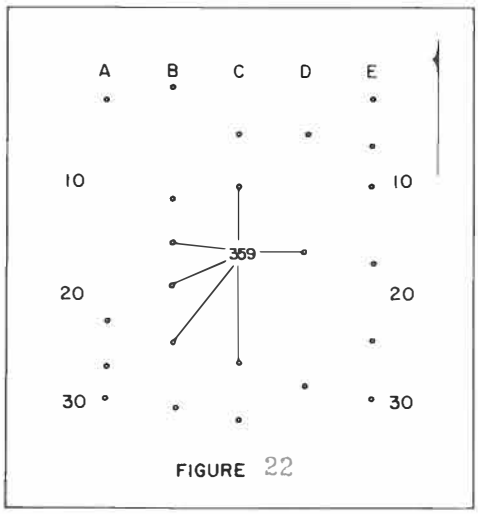


FIGURE 22

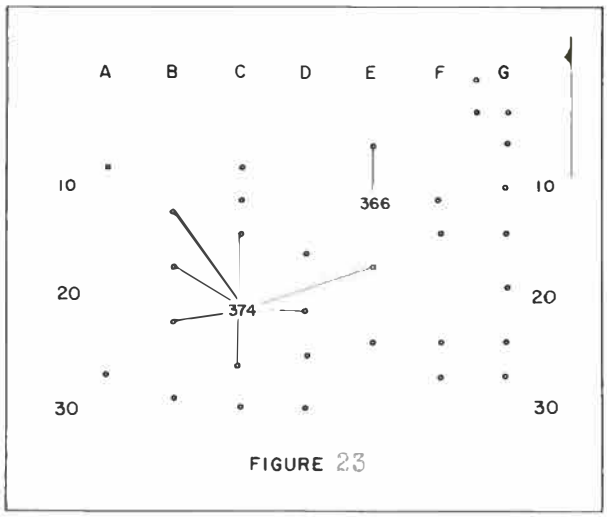


FIGURE 23

DIAGRAMS OF RED-HEADED PINE SAWFLY LARVAL MIGRATION PATTERNS FROM NATURALLY INFESTED TREES IN ONE-FOOT JACK PINE SANDFLOW PLANTATION.

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Migrations from tree 366 began two days after migration from tree 374 was completed. One larva was observed on tree K-6 and 42 dead in a depression in the sand near the host tree. These dead larvae were observed succumbing to high sand temperature caused when the direct sun rays penetrated a cloud cover and soil surface temperature rose to 127° F.

(Sod Plantations - Jack Pine)

Trees 618-619. Five colonies of second instar red-headed pine sawfly larvae were introduced on June 29 on two 1-foot jack pines growing in a sodded area adjacent to the 1-foot jack pine plantation discussed above. Stripping of these trees was completed 3 and 4 days later. On the day defoliation was completed, migrating larvae were observed leaving the host tree and on the sod at distances as great as 54 inches from the host tree. Figure 24 illustrates the infestation pattern of adjacent trees attacked. Four trees in the vicinity of tree 618 were infested with larvae as follows:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
H-9	9	4
H-14	150	2
H-17	1	5
I-16	3	7

Three trees in the vicinity of tree 619 were infested with larvae as follows:

Host Tree	Number of Larvae	Distance from Host Tree (Feet)
G-25	Approx. 150	6
D-21	1	7
D-27	1	10

Ants took a heavy toll among the migrating sawfly larvae. Survival among the migrating larvae was high, however, with approximately 160 larvae from tree 618 and approximately 150 from tree 619 successfully establishing themselves on adjacent trees. Migration from the newly infested trees was interrupted by disease. The average migration distance from the host tree on sodded terrain was nearly 6 feet with a maximum of 10 feet, the distance to the available nearby trees.

(Sod Plantation - Red Pine)

Larval migration studies on the 2-foot red pine plots were undertaken in a sod plantation. Defoliation of the 2-foot red pines was completed approximately one week later than that on the 1-foot plots and migration correspondingly delayed. Figure 25 presents a diagram of the study area and Table 9 a listing of the trees attacked by migrating

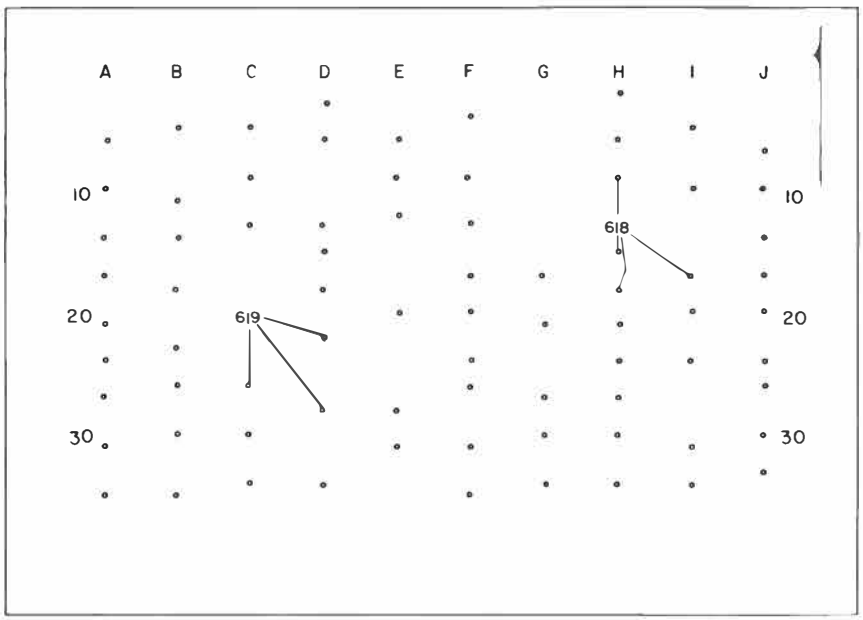

FIGURE 24. DIAGRAM OF RED-HEADED PINE SAWFLY LARVAL MIGRATION PATTERNS FROM ARTIFICIALLY INFESTED TREES IN ONE-FOOT JACK PINE SOD PLANTATION.

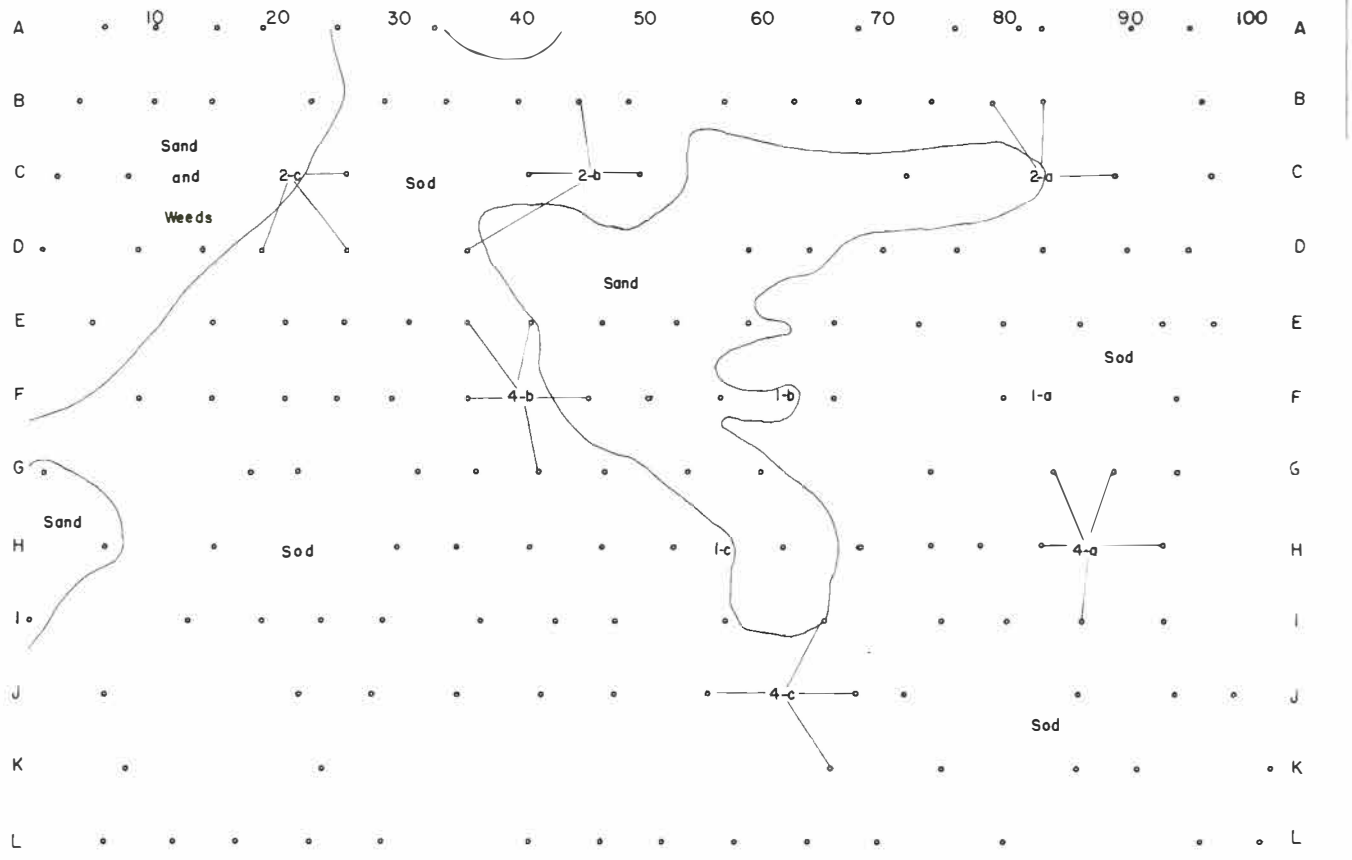

FIGURE 25. DIAGRAM OF RED-HEADED PINE SAWFLY LARVAL MIGRATION PATTERNS IN TWO-FOOT RED PINE PLANTATION.

LEGEND

Red pine tree °

Original host tree 4-a

Larval migration path ——

Distances in feet

TABLE 9. TWO-FOOT RED PINE TREES ATTACKED BY MIGRATING RED-HEADED PINE SAWFLY LARVAE

HANISTEE NATIONAL FOREST
- 1949 -

Host Tree	Attacked Tree	Distance from Host Tree (Feet)	Number of Larvae	Percent Defoliation
1-a	G-64	7	65	12
	G-69	7	40	25
(5 trees)	H-63	4	80	100
	H-93	6	14	6
	I-86	6	14	12
	Average =	6.0	213	
1-b	E-36	8	36	3
	E-42	7	125	100
(5 trees)	F-36	7	7	-
	F-46	6	33	3
	G-42	7	2	-
	Average =	7.0	203	
1-c	I-65	7	60	12
	J-56	6	36	25
(4 trees)	J-60	6	6	-
	K-66	7	80	25
	Average =	4.5	182	
2-a	B-79	8	1	-
	B-83	6	16	6
(3 trees)	C-89	6	5	-
	Average =	6.6	22	
2-b	B-45	6	29	6
	C-41	5	80	50
(4 trees)	C-50	4	5	-
	D-36	11	9	-
	Average =	6.5	114	
2-c	C-26	5	5	-
(3 trees)	D-19	7	2	-
	D-26	8	2	-
	Average =	6.6	9	

larvae. Complete defoliation of the 4- and 2-colony trees was encountered and migrating larvae successfully established themselves on nearby trees. No migration from the 1-colony trees was encountered as defoliation did not progress to completion on these trees. Larval migrants from the trees infested with 4- and 2-colonies attacked 24 trees up to 11 feet from the host tree. No mortality due to high surface temperatures was encountered. A few larvae were observed being attacked by ants; the significance of this factor was not determined. The spread of the larvae from the 2-foot host tree in the sod plantation was not as great as from the sand growing trees. Also, greater numbers of larvae established themselves on the new host trees. Severe defoliation was encountered on 3 of the 18 trees.

Summary. Following the completion of defoliation, red-headed pine sawfly larvae were observed to remain on their host tree from 1 to 4 days. After leaving the host tree they were able to successfully traverse distances up to 19 feet across bare sand to re-establish themselves on nearby pines if high soil surface temperatures did not interfere. Further migrations from these second hosts were made if defoliation was again completed. Heavy mortality from high surface temperatures was often encountered among larvae migrating across bare blow sand. Larvae entrapped in shallow depressions generally failed to escape and died when direct sunlight raised surface temperatures to the lethal (-105° F.) range.

Survival among larvae migrating across sodded areas was very high. The larvae tended to spread only to the immediately adjacent trees and to arrive in greater numbers on the new host. Although no mortality due to high surface temperatures was encountered, some loss to ants was observed; the significance of this loss was not determined.

Table 10 presents the ratio of trees attacked per tree infested on the study plots. Examination of this table indicates that the greatest number of trees were infested by migrants on the sandblow plantations. Although the average unweighted distance of migration was greater across the sandblow areas than across sodded areas, the greater number of larvae successfully established themselves after migrating across the sodded area. The success during migration across sandblows was mainly influenced by the presence or absence of direct sunlight during this critical period.

The rapidity with which these small host trees were stripped of their foliage by the large larval populations and the subsequent severe defoliation injury to the adjacent pines by the migrants presented a clear example of the intra-specific self limiting tendency of high insect populations when their food supply is saturated. If the entire plantation had been infested at the 2 colony level, intra-specific competition would certainly have resulted in a drastic population reduction through starvation.

TABLE 10. RATIO OF NUMBER OF TREES ATTACKED BY MIGRATING RED-HEADED PINE SAWFLY LARVAE TO TREES ARTIFICIALLY INFESTED MARITIME NATIONAL FOREST - 1949

Plantation	Original Infestation (Trees)	Final Infestation (Trees)	Average Distance* (Feet)	Ratio of Final/Original Infestation
Sandblow				
1-ft. Jack Pine				
4 colony	3	21	7.4	7.0/1
2 "	3	28	9.8	9.7/1
1 "	3	23	7.3	7.7/1
1-ft. Red Pine				
4 colony	3	29	8.9	9.7/1
2 "	3	18	7.6	6.0/1
1 "	3	5	6.0	1.7/1
Sodded				
1-ft. Jack Pine	2	7	5.8	3.5/1
2-ft. Red Pine				
4 colony	3	14	6.3	4.7/1
2 "	3	10	6.6	3.3/1
Natural Infestation				
Sandblow - 1-ft.				
Jack Pine	4	19	7.2	4.7/1

* Not weighted.

Parthenogenetic Reproduction and Sex Ratio

Atwood and Peck (1943) and Daviault (1949) reported successful parthenogenetic reproduction by the red-headed pine sawfly. Arrhenotoky is the rule in the genus Neodiprion and only males have been obtained from virgin reproduction.

The ratio of females to males has been reported to be as follows by Canadian and American workers:

	Females	Males	
Quebec, Canada	44	56	Daviault (1949)
Ontario, Canada	69	31	Brown (1942)
East Falls Church, Virginia	75	25	Middleton (1921)
Southern Illinois - First Gen.	84	16	
" " Second "	82	18	
" " - Third "	81	19	

NATURAL CONTROL FACTORS

A number of parasitic and predatory insects have been reported attacking the red-headed pine sawfly in eastern North America. These entomophagous insects undoubtedly exert considerable influence on the population dynamics of the sawfly. Little quantitative information is available, however, concerning the importance of these insects in the United States and Canada. The majority of the references to parasitism of the red-headed pine sawfly cite only the occurrence of various species collected in the field or reared from larval or cocoon collections.

In the United States Middleton (1921), Greene (1921), Pellvin [1] and Schaffner [2] have listed the parasites attacking the red-headed pine sawfly, but present no quantitative data concerning the effectiveness of the species recovered. In Canada, Brown (1942) reported "cocoon parasitism" intensities of 15, 16, 21, 30 and 18 percent from 1937 through 1941, but failed to indicate the relative importance of 16 species concerned. Lavialt's unpublished studies (1939) on the sawfly and its parasites in Quebec, Canada are probably the most complete to date. Lavialt has kindly made available unpublished data containing a list of 24 parasites and predators attacking the red-headed pine sawfly. He states that "only a few species play an important role in controlling the sawfly." He found two Diptera, Spathimeigenia aurifrons Curran and Phorocera lunata A. & W. to be the most important parasites attacking the red-headed pine sawfly. The effectiveness of these two parasites was markedly reduced by the hyperparasite Perilampus hyalinus Say. Table 11 is a summary of the parasitism attributed to the two Dipterous species and other parasites. Spathimeigenia accounted for 13.9 percent in 1937, and 37.6 percent and 13.7 percent in 1938 and 1941 respectively. Phorocera accounted for 16.2, 5.1, and 24.3 percent in 1937, 1938, and 1941 respectively. Hymenopterous parasites were of little significance in the population dynamics. Exeristes canadensis Prov., Glenoscopa lophyri (Riley), and Lemophus contortionis Davis were the most prevalent species. The hyperparasite Perilampus hyalinus Say was of major importance constituting 68.3, 51.6, and 53.9 percent of the non-sawfly emergents in 1937, 1938, and 1941 respectively.

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[1] Correspondence

TABLE 11. PARASITES REARED FROM NEODIPRION LECONTEI (FITCH) IN QUEBEC, CANADA. (DEWITT 1949)

Species	No.	Percent	No.	Percent	No.	Percent
Spathimeigenia aurifrons Curran	43	13.9	1,913	37.6	23	14.7
Phorocera hanata A. & T.	50	16.2	262	5.1	38	24.3
Total	93	30.1	2,175	42.7	61	39.0
Megaselia proboscidea (Mall.)			57	1.1		
Ichneumonidae	4	1.3	232	4.5	11	7.1
Chalcididae	1	0.3	5	0.1		
Perilampus hyalinus Say	211	68.3	2,622	51.6	84	53.9
Total	309	100.0	5,091	100.0	156	100.0
Basis*	1,116	27.7	10,932	46.6	520	30.0

* Larvae collected less larvae dead and in diapause.

Egg Parasitism

Studies conducted by the writer on the Shawnee National Forest in 1947, 1948, and 1949 indicated that the egg parasite Closterocerus cinctipennis Ashm. was one of the most important biotic factors limiting red-headed pine sawfly populations on that Illinois Forest. Pre-spray sawfly population estimates based on an egg survey conducted early in 1947 indicated high sawfly populations on approximately 6,000 acres of shortleaf pine plantations. Re-examination of these plantations a few days before aerial spraying operations were to be initiated revealed that a marked reduction in larval hatch had occurred. As a result of this reduced hatch, 1,900 acres of heavily infested pine plantation were deleted from the spray schedule. Sawfly egg collections made on 4 of the 13 plantations showing reduced hatch were heavily parasitized by Closterocerus. Table 12, a summary of the parasitism on these 4 plantations, is based on 20 egg batches of 4,154 eggs. Egg parasitism on these plantations ranged from 70.3 percent to 93.1 percent and averaged 88.7 percent. One hundred percent egg parasitism was encountered in 4 of the 20 egg batches.

TABLE 12. RED-HEADED PINE SAWFLY EGG PARASITISM BY *CLOSTEROCERUS CINCTIPENNIS* ASHM. DURING FIRST GENERATION ACTIVITY SHAWNEE NATIONAL FOREST - 1947

Location T-S	R-E	Sec.	Total Egg Batches	Total Eggs	Parasitized Eggs	Percent Parasitism
13	5	4	6	2,450	2,282	93.1 ± 4.0
10	9	19	5	823	736	89.4 ± 5.8
12	6	16	3	594	428	70.3 ± 9.7
9	8	14	6	287	247	86.1 ± 6.7
Total			20	4,154	3,683	88.7 ± 5.7

An intensive egg parasite survey of the sawfly infested shortleaf pine plantations on the Shawnee National Forest following development of the second generation sawflies was not conducted owing to the urgency of experimental and commercial aerial control programs and subsequent evaluation activities. However, one small isolated roadside planting of approximately 40 pitch pine trees was carefully examined for egg parasitism. This small planting had been under heavy sawfly attack during the first generation in 1947. All second generation red-headed pine sawfly egg batches on 5 trees were collected for egg parasitism determination. Table 13 summarizes the parasitism of the 138 egg batches and 14,178 eggs examined in this study. Parasitism per tree ranged from 91.1 percent to 99.4 percent. Seventy-two of the 138 egg batches were 100 percent parasitized.

This plot of 5 pitch pine trees was examined periodically for the presence of sawfly eggs and egg parasitism during the remainder of 1947 and during the 1948 and 1949 field seasons. Two egg batches collected on tree 162 after the third generation sawfly flight in 1947 had an average parasitism of 94.9 percent.

Four of the 5 pitch pines were oviposited on during the first generation sawfly flight in 1948. Parasitism of the 9 batches of 1,280 eggs laid during this period averaged 98.5 percent (Table 14). Parasitism of the 6 egg batches on tree No. 161 averaged 96.7 percent. Parasitism of the single batches of eggs on the other 3 trees ranged from 6.1 percent to 96.6 percent. A single egg batch collected on tree No. 164 after second generation sawfly flight in 1948 was 98.0 percent parasitized. Two egg batches were collected on tree No. 164 during 1949. All 224 eggs laid during the second and third generation adult flight were parasitized.

TABLE 13. RED-HEADED PINE SAWFLY EGG PARASITISM BY *CLOSTEROCERUS CINCTIPENNIS* ASHM. ON ROADSIDE PITCH PINE PLANTATIONS - SHAWNEE NATIONAL FOREST - 1947

Tree No.	Total Egg Patches	Total Eggs	Parasitised Eggs	Percent Parasitism
		Second Generation		
161	12	1,677	1,587	94.6 ± 2.2
162	30	4,193	3,823	91.1 ± 2.3
163	34	3,930	3,833	97.5 ± 0.9
164	25	2,904	2,861	98.5 ± 0.4
165	17	1,474	1,466	99.4 ± 0.5
Total	138	14,178	13,570	95.7 ± 1.6
		Third Generation		
162	2	276	262	94.9

TABLE 14. RED-HEADED PINE SAWFLY EGG PARASITISM BY *CLOSTEROCERUS CINCTIPENNIS* ASHM. ON ROADSIDE PITCH PINE PLANTATIONS - SHAWNEE NATIONAL FOREST - 1948, 1949

Tree No.	Total Egg Patches	Total Eggs	Parasitised Eggs	Percent Parasitism
		First Generation		
161	6	695	672	96.7
162	1	151	146	96.6
163	1	353	310	87.8
164	1	81	5	6.1
Total	9	1,280	1,133	88.5
		Second Generation - 1948		
164	1	103	101	98.0
		Second - Third Generation - 1949		
164	2	224	224	100.0

No attempt was made to determine sawfly or parasite egg fertility, larval or cocoon parasitism, or predator activity on the foregoing roadside plantations. It was felt that on such a limited site, more could be learned concerning the potentialities of Closterocerus by allowing the sawfly infestation to progress with as little disturbance as possible. Egg parasitism determinations for any particular sawfly brood were, therefore, delayed until adult parasite emergence had occurred and the next generation sawfly egg population had been attacked. Third generation sawfly eggs were collected in late fall after sawfly hatch had taken place.

Table 15 presents a composite summary of the potential red-headed pine sawfly threat on the foregoing pitch pine plantation (based on egg batches and total number of eggs) and the resistance applied to this sawfly population by the egg parasite Closterocerus cinctipennis.

At the end of the second generation sawfly flight period in 1947, 138 batches of sawfly eggs representing a total of 14,178 potential larvae were present on the five pitch pine trees. Egg parasitism of 95.7 percent reduced the potential to 608 eggs, 456 of which could, if they survived, produce female sawflies the next generation. The 1:4 sex ratio was selected as an approximation since the sex ratio of the emerging sawflies on the Shumee was of this magnitude.

Emergence of a partial third generation of sawflies occurred in 1947 in which 2 egg batches of 276 eggs were laid on one tree. The appearance of these two females theoretically represented survivors of a combined mortality and diapause of 99.98 percent of the total second generation egg population. Ninety-four and nine-tenths percent egg parasitism reduced the potential to 14 eggs, 10 of which could be expected to produce female sawflies the following generation in 1948.

Nine egg batches were collected after the first generation sawfly adult flight in 1948. These nine batches of 1,280 sawfly eggs suffered an 88.5 percent egg parasitism and presented a potential of 110 females for the next generation. One egg batch was observed following second brood adult sawfly flight in 1948. A 96.0 percent parasitism reduced the potential of 103 eggs to one female possibility. No third generation adult sawflies were observed in this plantation in 1948.

TABLE 15. INFLUENCE OF EGG PARASITE CLOSTEROCERUS CINCTIPENNIS ASHM. ON RED-HEADED PINE SAWFLY POPULATION IN ROADSIDE PITCH PINE PLANTATION - SHAWNEE NATIONAL FOREST 1947 - 1948 - 1949

Year	Generation	Total Egg Batches	Total Sawfly Eggs	Percent Parasitism	Remaining Eggs	Potential Female Sawflies (1:1 sex ratio)
1947	Second	138	14,178	95.7	608	456
	Third	2	276	94.9	14	10
1948	First	9	1,280	88.5	147	110
	Second	1	103	98.0	2	1
1949	Second					
	Third	2	224	100.0	0	
	Total	152	16,061	95.2	771	

Two egg batches of 224 eggs were collected on one tree during 1949. All of these eggs were parasitized.

During the two and three-quarter years the red-headed pine sawfly population was followed on the pitch pine plot, 152 egg batches containing 16,061 eggs were laid on the five pines. Ninety-five and two-tenths percent or 15,290 of these eggs were parasitized during this period. The remaining 771, or 4.8 percent, of the population was accounted for during the season by other factors such as: egg infertility, parasitism, predation, disease, climatic factors, diapause, and imponderables.

Returning to the role of the egg parasite Closterocerus on the Shawnee pine plantations, egg parasitism of 88.7 percent ± 5.7 percent occurred on 4 of 13 plantations surveyed during first generation sawfly activity in 1947. As has been outlined in the foregoing discussion, egg parasitism determinations were not undertaken on a forest-wide basis during second generation in 1947. Intensive examination of the one roadside pitch pine planting revealed an average egg parasitism of 95.7 percent. In addition, attempts to rear the red-headed pine sawfly from fertilized and unfertilized eggs were unsuccessful on three widely scattered plantings. Egg parasitism determinations were not made on these plantings.

Third generation sawfly activity on the Shawnee National Forest in 1947 was markedly reduced when a high percentage of the second generation larvae went into diapause. Third generation adult emergence from larval collections made on 7 shortleaf pine plantations under heavy sawfly attack during the second generation averaged 5.6 percent with 90.4 percent remaining in diapause. Sawfly eggs were collected on 8 plantations throughout the forest to determine the influence of the egg

parasite Closterocerus during third generation adult sawfly activity. Table 16 summarizes the findings of this survey. Egg parasitism averaged 87.1 ± 5.2 percent throughout the 8 plantations surveyed and ranged from 58.5 to 99.7 percent. Twenty-five of the 80 egg batches were 100 percent parasitized.

TABLE 16. RED-HEADED PINE SAWFLY EGG PARASITISM BY CLOSTEROCERUS CINCTIPENNIS ASHM. DURING THIRD GENERATION ON SHORTLEAF PINE PLANTATIONS - SHAWNEE NATIONAL FOREST - 1947

Location T-S	Location R-E	Location Sec.	Total Egg Batches	Total Eggs	Parasitised Eggs	Percent Parasitism
10	8	27	13	2,187	2,134	97.6 ± 1.3
10	7	25	13	1,403	1,361	97.1 ± 1.7
11	5	34	11	1,273	745	58.5 ± 7.9
11	6	35	6	1,015	857	84.4 ± 7.7
12	6	18	14	1,853	1,446	78.1 ± 6.5
12	6	19	3	440	423	96.2 ± 1.6
12	6	19	10	894	756	84.6 ± 4.8
12	5	32*	10	1,410	1,405	99.7 ± 0.2
	Total		80	10,475	9,127	87.1 ± 5.2

* Jack pine planting included.

Red-headed pine sawfly populations were very low throughout the Shawnee National Forest in 1948. Sawfly activity was observed only in the most favorable ecological sites such as in shaded areas and on widely spaced pines. Sawfly egg collections were made on 13 shortleaf pine plantations throughout the forest to determine the first generation sawfly egg parasitism. The average parasitism by Closterocerus for 86 egg batches of 9,311 eggs was 79.3 ± 6.1 percent (Table 17). Parasitism ranged from 25.4 to 96.5 percent. Thirty of the 86 egg batches were 100 percent parasitized and 3.8 percent of the eggs were eaten by some unidentified predator.

TABLE 17. RED-HEADED PINE SAWFLY EGG PARASITISM BY CLOSTEROCERUS CINCTIPENNIS ASHM. DURING THE FIRST GENERATION ON SHORTLEAF PINE PLANTATIONS - SHAWNEE NATIONAL FOREST - 1948

Location T-S	R-E	Sec.	Total Egg Batches	Total Eggs	Parasitized Eggs	Eggs Destroyed*	Percent Parasitism
10	6	29	15	2,019	1,892	19	93.8 ± 3.3
10	6	29	2	213	171	42	80.3 ± 18.1
10	6	32	5	648	583	6	90.0 ± 8.1
10	7	25	10	781	758	56	97.1 ± 1.1
10	8	9	8	805	513	50	63.6 ± 12.2
10	8	27	3	321	257	22	80.0 ± 5.7
11	5	26	2	126	69	—	54.8 ± 2.6
11	5	34	10	1,233	1,154	70	93.6 ± 3.4
11	6	11	2	204	176	10	87.2 ± 6.8
11	7	31	15	1,147	360	19	25.4 ± 10.1
12	6	18	6	576	556	—	96.5 ± 2.9
12	6	19	2	325	300	10	92.3 ± 1.7
12	6	18 & 19	6	643	596	41	92.7 ± 2.8
Total			86	9,311	7,386	354 (3.8 percent destroyed)	79.3 ± 6.1

* Destroyed by unknown predator

Second generation sawfly activity was observed on only 4 plantations. The average parasitism of 7 egg batches collected containing 804 eggs was 80.6 ± 15.9 percent (Table 18). Egg parasitism was further augmented by predation by some unknown predator averaging 11.2 percent. The 11.2 percent predation included part of the eggs parasitized by Closterocerus.

Egg collections were possible on only 3 plantations during third generation activities in 1948 due to the low sawfly population. The average parasitism of 11 egg batches of 1,481 eggs by Closterocerus was 81.4 percent (Table 19). Predation by some unknown predator accounted for an average of 16.5 percent, which brought the total egg destruction to 97.9 percent.

Sawfly egg parasitism was not determined on the shortleaf pine plantations during early 1949 because of the exceedingly low sawfly population and the difficulty in collecting sawfly eggs. Twenty-eight shortleaf pine plantations, examined on two ranger districts, appeared free of sawfly activity. Ovipositing female sawflies were observed on two shortleaf pine plantations within the "pine hills" native shortleaf range. Closterocerus adults were observed ovipositing in the newly laid sawfly eggs.

Closterocerus cinctipennis adults have been reared from red-headed pine sawfly eggs on the Park Falls ranger district of the Chequamegon National Forest in north central Wisconsin and on the Cadillac ranger district of the Manistee National Forest in central Michigan. The importance of this parasite in reducing the sawfly hatch was not determined. Cursory examination of plantations throughout these two north central forests indicated, however, that egg parasitism was of minor significance.

TABLE 18. RED-HEADED PINE SAWFLY EGG PARASITISM BY CLOSTEROCERUS CINCTIPENNIS ASHM. DURING THE SECOND GENERATION ON SHORTLEAF PINE PLANTATIONS - SHAWNEE NATIONAL FOREST - 1948

Location T-S	R-E	Sec.	Total Egg Batches	Total Eggs	Parasitized Eggs	Destroyed Eggs	Percent Parasitism
10	6	33	3	445	399	7	89.7 ± 1.6
10	7	25	1	87	31	47	35.6
11	7	31	2	192	187	—	97.4
12	6	19	1	80	31	36	38.7
Total			7	804	648	90 : 11.2 per- cent	80.6 ± 15.9

TABLE 19. RED-HEADED PINE SAWFLY EGG PARASITISM BY CLOSTEROCERUS CINCTIPENNIS ASHM. DURING THE THIRD GENERATION ON SHORTLEAF PINE PLANTATIONS, SHAWNEE NATIONAL FOREST-1948

Location T-S	R-E	Sec.	Total Egg Batches	Total Eggs	Parasitized Eggs	Destroyed Eggs	Percent Parasitism
10	6	29	1	191	180	-	94.2
10	7	25	5	597	337	241*	56.4
11	7	31	5	693	689	4*	99.4
Total			11	1,481	1,206	245* : 16.5 per- cent	81.4

* May include parasitized eggs.

A few species of the egg parasite Tetrastichus sp. were reared from red-headed pine sawfly eggs on the Shawnee National Forest during 1947, 1948, and 1949. These parasites appeared to be of negligible significance in reducing the sawfly egg population.

Larval Parasitism

Six species of parasites were reared from red-headed pine sawfly larvae on the Shawnee National Forest during 1947 and 1948. Of these, Spathimeigenia spinigera Tns. and Phorocera hamata A. & W. appeared to be of greatest importance. Table 20, a summary of emergence from reared cocoons in 1947, indicated total larval parasitism by all 6 species averaged 42.2 percent during the first generation. Parasitism of second generation larvae averaged 40.5 percent in the 1947 emergents and 28.1 percent in 1948 emergents of these 1947 second generation larvae. Spathimeigenia spinigera Tns. accounted for 76.2 percent, 78.9 percent, and 94.9 percent of these parasites; Phorocera hamata A. & W. accounted for 13.3 and 16.9 percent of the 1947 emergents. No Phorocera were recovered from the overwintering 1947 second generation larvae.

The hymenopterous parasites Lamachus contortionis Davis, Agrothereutes lophyri (Kort.), Endasys subclavatus (Say), and Olesicampe lophyri (Riley) were recovered during 1947. The hyperparasites, Perilampus hyalinus Say, Mellitobia acasta (Walk.), Dibrachys cavus (Walk.), and Trichopria sp. were also recovered but were of little significance in the parasite picture.

Detailed parasite rearing studies were not conducted on the Manistee National Forest during the 1946-1948 outbreak. Of the 8 species reared and collected on this Forest by the writer during 1948, Phorocera hamata A. & W. appeared to be the most important Diptera, and Exenterus canadensis Prov., N. diprioni Rohw., and Lamachus contortionis Davis, the most important Hymenoptera. The hyperparasite Perilampus hyalinus Say was very active throughout 1948 and 1949 and was probably of great significance.

TABLE 20. PARASITES REARED FROM RED-HEADED PINE SAWFLY COCOONS ON THE SHAWNEE NATIONAL FOREST - 1947

Species	First Brood 1947 Number	First Brood 1947 Percent	Second Brood - 1947 Emergents 1947 Number	Second Brood - 1947 Emergents 1947 Percent	Emergents 1948 Number	Emergents 1948 Percent
Spathimeigenia spiniger Tns.	703	76.2	179	78.9	505	94.9
Phorocera hamata	122	13.3	43	18.9	-	-
A. & H.	825	89.5	222	97.8	505	94.9
Hymenoptera						
Leucibus contortionis						
Davis	4	0.4	5	2.2	1	0.2
Agrotheretes lophyri (Hort.)	69	7.5				
Endasys subclavatus (Say)	6	0.6				
Olesicampe lophyri (Riley)					1	0.2
Perilampus hyalinus (Say)	10	1.1			8	1.5
Miscellaneous hyper parasites	8	0.9			17	3.2
	97	10.5	5	2.2	27	5.1
Total	922	100.0	227	100.0	532	100.0
Basis*	2,187	42.2	560	40.5	1,892	28.1

* Total cocoons minus dead and diapausing individuals.

Predator activity has been commonly observed in many localities throughout the range of the sawfly. Twelve species of predators have been recorded attacking the adult and larval stages of the sawfly; 8 were collected in the United States and 2 in Canada. Davisult (1919) also listed 2 undetermined species of predators attacking the red-headed pine sawfly in Canada. No birds have been recorded feeding on the larvae or adults of the sawfly. The importance of rodents in the predatory picture was not determined. Trapping on both the Shawnee and Manistee Forests was not productive. Few rodents were captured during trapping studies on the Manistee National Forest and few signs of their activity were observed.

Heavy larval mortality caused by disease was observed on the Manistee National Forest and defoliation studies were interrupted during 1949 when large numbers of larvae succumbed to this unknown disease.

Four attempts to introduce the Chalcid prepupal parasite Microplectron fuscipennis Zett. into the United States were made during the past 10 years. In the first attempts, 300,000 parasites were released in northern Alabama in 1940 and 280,000 in western Tennessee along the Tennessee Valley Authority reservoir pine plantings in 1941 (Zimmerman).1/ No information concerning the success of these two introductions, nor from an attempt in 1941 to introduce this parasite on the Manistee National Forest has been published. The fourth attempt to introduce Microplectron into the United States was made on the Manistee National Forest in 1946. A total of 100,000 adult parasites were liberated in 7 plantations. Adult parasites were recovered from limited cocoon collections in 1947. Subsequent collections have been negative. The difficulty encountered collecting cocoons of the red-headed pine sawfly probably accounts for the meager recovery data following these liberations.

In summary, 58 parasitic and predatory species of insects have been reported attacking the red-headed pine sawfly in eastern North America. Of these entomophagous insects 21 have been collected exclusively in the United States, 23 exclusively in Canada, and 14 in both the United States and Canada. Table 21 lists the parasitic and predatory insects attacking the sawfly in North America. The hyperparasites of the sawfly are also included in this list. This list, assembled from the literature and correspondence with United States and Canadian entomologists and from collection records of the Milwaukee Forest Insect Laboratory, has been corrected by Mr. C. F. W. Muesebeck of the Division of Insect Identification, U. S. Bureau of Entomology and Plant Quarantine.

1/ Correspondence

TABLE 21. PARASITES AND PREDATORS ATTACKING THE RED-HEADED PINE SAWFLY IN EASTERN NORTH AMERICA

Order	Species (Parasites)	Country	Observer
I. Diptera	Bessa harveyi Tns.	Canada	Brown (1942)
	Hylotomasyia hylotomae (Coq.)	U. S.	Greene (1921) *Schaffner
	Megaselia proboscidea (Zett.)	Canada Canada	Brown (1942) Davisult (1949)
	Megaselia pulicaria (Fall.)	Canada	Brown (1942)
	Musina assimilis (Fall.)	Canada	Davisult (1949)
	Pelecotheca aenea (Vander Wulp)	U. S.	Middleton (1921) *Busseboek
	Phorocera claripennis Macq.	U. S. U. S.	Greene (1921) *Schaffner *Busseboek
	Phorocera hunata A. & W.	U. S. U. S. Canada Canada Canada	*Benjamin *Schaffner Davisult (1942,1949) *Bradley Brown (1942)
	Spathimeigenia aurifrons Curran	U. S. Canada Canada Canada	*Schaffner Davisult (1949) *Bradley Brown (1942)
	Spathimeigenia cracta Ald.	Canada Canada Canada	Davisult (1949) *Bradley Brown (1942)
	Spathimeigenia spinigera Tns.	U. S. U. S. U. S. U. S. U. S. U. S. U. S. U. S. U. S. U. S. U. S. Canada	Aldrich (1931) Greene (1921) Middleton (1921) Bentley (1940) Sellers (1940) *Olivia *Schaffner *Busseboek *Orr *Zimmerman *Benjamin *Bradley

Table 21 - (continued)

Order	Species	Country	Observer
I. Diptera (Cont.)	Ville simuosa, Wied.	U. S.	*Blair
	Spathimeigenia sp.	U. S.	*Benjamin
	Zenillia sp.	Canada	Davisult (1949)
II. Hymenoptera	Agrothereutes lophyri (Nort.)	U. S.	Bentley (1940)
		U. S.	*Benjamin
		U. S.	*Zimmerman
		Canada	Davisult (1949)
	Amblymerus verditer (Nort.)	Canada	Davisult (1949)
	Aptesis indistincta (Prov.)	U. S.	*Schaffner
		Canada	Brown (1942)
	Closterocerus cinctipennis Ashm.	U. S.	*Benjamin
	Delomerista diprionis Cush.	Canada	Davisult (1949)
	**Dibrachys clavus (Walk.)	U. S.	*Benjamin
		Canada	Davisult (1949)
	Eulasys subelevatus (Say)	U. S.	Bentley (1940)
		U. S.	*Benjamin
		U. S.	*Schaffner
		U. S.	*Zimmerman
		Canada	Davisult (1949)
	Exenterus auicterius (Panzer)	U. S.	Sellers (1940)
	Exenterus canadensis Prov.	U. S.	Townes (1944)
		U. S.	*Muesebeck
		U. S.	*Benjamin
		Canada ?	Walley (1933)
		Canada	Davisult (1942,1949)
		Canada	Brown (1942)
	Exenterus diprioni Rohw.	U. S.	Middleton (1921)
		U. S.	*Orr
		U. S.	Cushman (1940)
		U. S.	*Benjamin
		U. S.	*Muesebeck
		U. S.	*Schaffner
		Canada	Rutchins (1926)
		Canada ?	Townes (1944)
		Canada	*Bradley

Table 21 - (continued)

Order	Species	Country	Observer
II. Hymenoptera (Cont.)	Lamachus contortionis Davis	U. S.	Rohwer (1915)
		U. S.	Chamberlain (1922)
		U. S.	Middleton (1921)
		U. S.	*Polivka
		U. S.	*Schaffner
		U. S.	*Muesebeck
		U. S.	*Benjamin
		Canada	Davisult (1942,1949)
		Canada	Brown (1942)
		Canada ?	Townes (1944)
		Canada	*Bradley
	Lamachus lophyri (Ashm.)	Canada	Brown (1942)
	Lamachus virginianus (Rohwer)	U. S.	Rohwer (1915)
		U. S.	Middleton (1921)
		U. S.	*Polivka
		U. S.	*Schaffner
		U. S.	*Muesebeck
		Canada	Brown (1942)
		Canada ?	Townes (1944)
	Mastrus sciculatus (Prov.)	Canada	Brown (1942)
	**Melittobia acasta (Walk.)	U. S.	*Benjamin
	Mesoleius submarginatus (Cress.)	U. S.	*Schaffner
		Canada	Brown (1942)
	Microbracon pygmaeus (Prov.)	U. S.	*Polivka
	Microplectron fuscipennis (Zett.)	U. S.	*Blair
	Olesicampe lophyri (Riley)	U. S.	*Schaffner
		U. S.	*Benjamin
		Canada	Davisult (1942-1949)
		Canada	Brown (1942)
	Orthocentrus nigricornis Prov.	Canada	Davisult (1949)
	Otacustes crassus (Prov.)	Canada	Davisult (1949)
	**Perilampus hyalinus Say	U. S.	Middleton (1921)
		U. S.	*Orr
		U. S.	*Schaffner
		U. S.	*Muesebeck
		Canada	Davisult (1949)
		Canada	*Bradley
		Canada	Brown (1942)
		U. S.	*Benjamin
	Perilampus hyalinus Say	Canada	*Watson

Table 21 - (continued)

Order	Species	Country	Observer
II. Hymenoptera (Cont.)	Plectiscidea carinata Prov.	Canada	Daviault (1949)
	Psychophagus omnivorus (Walk.)	Canada	Daviault (1949)
	Asoplex sp.	Canada	Daviault (1949)
	Calis sp.	Canada	Daviault (1949)
	Hemiteles sp.	Canada	Daviault (1949)
	Mesochorus sp.	Canada	Daviault (1949)
	Orthostigma sp.	Canada	Daviault (1949)
		Canada	Brown (1942)
Undescribed Species	**Trichopria n. sp.	U. S.	*Benjamin
	Tetrastichus sp.	U. S.	*Benjamin
	Agrotheretes sp.	U. S.	*Benjamin
	PREDATORS		
Hemiptera	Apateticus bracteatus (Fitch)	U. S.	*Benjamin
	Apiomerus crassipes (F.)	U. S.	*Benjamin
	Arilus cristatus (L.)	U. S.	*Polivka
		U. S.	*Benjamin
	Rabis ferus (L.)	Canada	Daviault (1949)
	Podisus serieventris Uhler	U. S.	*Benjamin
	Psalliopus cinctus (F.)	U. S.	*Polivka
	Sinea diadema (F.)	Canada	Daviault (1949)
Diptera	Zelus socius Uhler	U. S.	*Benjamin
	Erax aestuans (L.)	U. S.	*Benjamin
Hymenoptera	Vespula maculifrons Rohw.	U. S.	*Benjamin
Hemiptera	Apateticus sp.	Canada	Daviault (1949)
(To Coleus)	Podius sp.	Canada	Daviault (1949)

* From correspondence and unpublished records of the Milwaukee Forest Insect Laboratory

** Hyperparasite

Climatic Factors

Climatic factors have been repeatedly reported as playing an important role in the population dynamics of the insects. Temperature and moisture extremes have been reported as the factors causing the decline of outbreak populations of many forest insects. Little information is available, however, concerning the influence of climatic factors on red-headed pine sawfly populations. In unpublished records made by L. W. Orr it was reported that heavy first instar larval mortality apparently due to high temperatures occurred on the Cadillac ranger district of the Manistee National Forest. Orr also noted high degrees of mortality among first and second instar larvae due to driving rains. Similar observations were made by the writer during 1949. Unpublished records by H. J. MacAloney noted "extremely heavy larval mortality in a blizzard in late October" during a red-headed pine sawfly outbreak in northern Michigan. This blizzard with its accompanying low temperatures and deep snow apparently reduced the red-headed pine sawfly population to an endemic status as "after the snow melted . . . literally millions of dead Neodiprion lecontei larvae were found under the trees."

The writer observed heavy first instar larval mortality in southern Illinois during 1947 when air temperatures remained above 100° F. for protracted periods of time. Heavy mortality caused by high temperatures was also observed on the Manistee National Forest among migrating larvae caught on bare sand during the heat of the day. Sand temperatures above 105° F. were common during the days when a light cloud cover was present and soil surface temperatures above 135° F. commonly occurred during clear days. Larval survival was less than 3 minutes on sand when surface temperatures were above 105° F. Heavy egg mortality due to an early June freeze in which temperatures fell to 18° F. was encountered on the Lower Michigan National Forest in 1949. Larvae survived temperatures as low as 22° F. on the Shawnee National Forest during 1947, however, and continued to feed when air temperatures again rose above 60° F.

ECOLOGICAL INVESTIGATIONS

Introduction

Studies of most insects of economic importance generally begin during an outbreak of the pest or after an outbreak has existed for some time and heavy economic losses have been sustained. Major emphasis is thus most frequently placed on the problem of curtailing further loss through reducing the current insect population. Ecological studies of less apparent or immediate importance are thereby deferred until the pressure of control or salvage activities has eased. Unless the insect remains currently important, these so-called minor phases may be delayed only to be re-delayed when a return to high population is again experienced several years later. Low population investigations, possibly the key to the reservoir or survival problem, are seldom undertaken and then only partially completed.

Red-headed pine sawfly investigations were begun on the Shawnee National Forest in 1947 and on the Manistee National Forest in 1948 after the sawfly had been in outbreak status for some time. Although the major

emphasis was initially on the control phases of the problem, opportunity was available to delve into the ecology of the outbreak populations as well as to follow closely their decline and subsequent activities of the low populations. Ecological investigations were conducted on the Shawnee National Forest during the 1947 outbreak and during the low population period in early 1948 and 1949. High population studies were also conducted on the Manistee National Forest in late 1948 and during low population levels in 1949. National forest areas under sawfly attack in Wisconsin, Minnesota, Missouri, Michigan, and Illinois were visited in 1948 and 1949 to obtain a region-wide picture of this insect. (Map 1).

High Population Investigations
Infestation vs. Defoliation

During the 1947 pre-spray survey of shortleaf pine plantations on the Shawnee National Forest infested by the red-headed pine sawfly, data were accumulated concerning the intensity of single generation (1946) defoliation at different infestation levels in unsprayed plantations. One of the primary objectives was to determine if a relationship existed between the percent infestation (number of trees infested per unit area) and the percent defoliation of these attacked trees. If such a relationship was found to exist, it was of major interest to determine where in the infestation intensity picture severe defoliation occurred. It was hoped that this percent infestation criterion could be used as a sound basis for predicting defoliation at various population levels, and subsequently be used for a more logical approach in preparing recommendations for the control of this insect with insecticides.

Thirty-five shortleaf pine plantations were included in the survey. A record was kept of all trees (22 trees per plot) on each of 4 plots per 40 acres examined. The height of the trees was estimated to the nearest foot. In estimating the percentage defoliation, a geometric progression was employed. The defoliation classes used were percentages of 0, 3, 6, 12, 25, 50, 75, 87, 93, 96, 99, and 100. The basic procedure followed in estimating the percent defoliation was to assign the tree to first a broad classification (that is, the defoliation above or below 50 percent) and next to assign it to its proper class through mental comparison with the next lower or higher defoliation category. An example may better explain the procedure and principle involved in estimating the defoliation of a given tree. Assuming an 87 percent defoliated tree was encountered, it would be immediately obvious that defoliation was present and that this defoliation was in excess of 50 percent. The next decision would place the defoliated tree between the 75 and 100 percent classes. The decision remaining would be to judge how much greater the defoliation was than 75 percent; that is, whether the defoliation was closer to 87 percent than to 75 or 100 percent. This particular example tree appeared to fall approximately between the two categories and was assigned, therefore, to the 87 percent defoliation class. The same procedure was followed in assigning defoliated trees to classes below the 50 percent level. Naturally, a small amount of indecision was encountered in assigning defoliated trees to classes between the 87 and 99 percent and to the class between the 12 and 3 percent categories when this defoliation estimate was first employed. The writer

and several associates compared defoliation estimates using this system and the more popular 10 percent interval system and, after an initial period of introduction, found estimates based on the geometric progression more consistent.

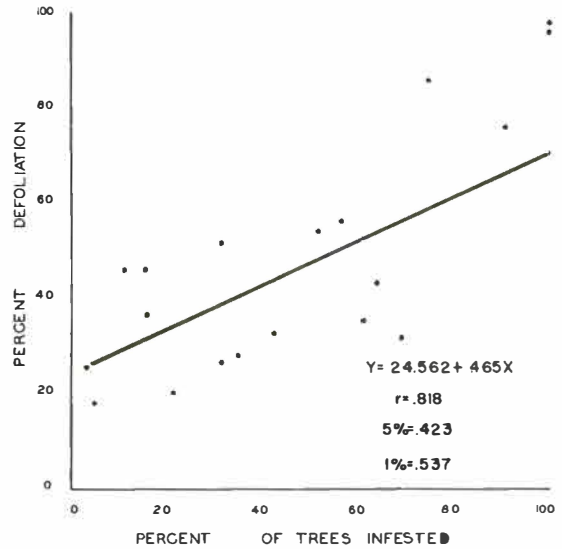
In analyzing the sawfly defoliation data collected during the pre-spray survey, the average height of each plantation was calculated and the plantations assigned to one of the following three height classes: 2.0 to 3.9 feet, 4.0 to 6.9 feet, and 7.0 feet and over. The percent infestation and percent defoliation of the attacked trees was calculated for each plantation. Statistical analysis of the infestation-defoliation data (Coefficient of Correlation) indicated a linear relationship between the percent infestation and the percent defoliation in the 2.0- to 3.9-foot class and in the 4.0- to 6.9-foot class. These two classes made up the majority of the plantations on the forest. No significant relationship was found to exist in the 7.0-foot and over class; the data in this class were too few for adequate statistical treatment. Fisher's Analysis of Variance was also applied to the data and suggested a very highly significant linear relationship between the infestation-defoliation data collected in the 2.0- to 3.9-foot class and in the 4.0- to 6.9-foot classes. Since no significant difference appeared to exist between the straight line and the curved line fitted through the data, a straight line (using the Coefficient of Correlation method) was used to show the relationship.

Graph 1 of the 4.0- to 6.9-foot class illustrates the increase in percent defoliation of attacked trees as the number of trees attacked increased. For example, at the 10 percent infestation level, an average of 28 percent defoliation was encountered. At the 50 percent level 48 percent defoliation was encountered and at the 75 percent infestation level, 58 percent defoliation occurred.

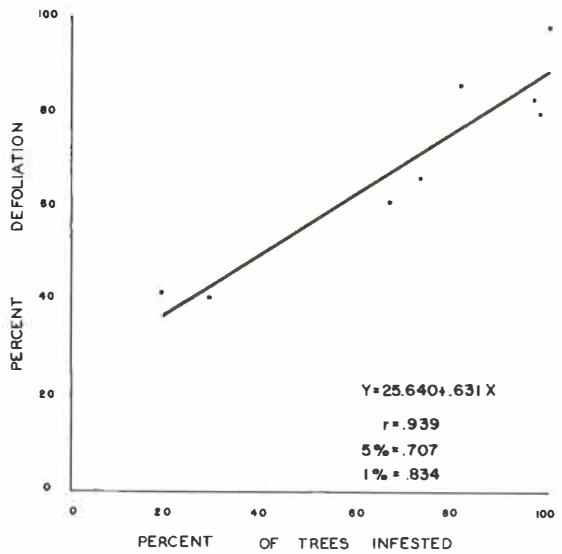
Graph 2 illustrates the relationship between defoliation and infestation on the 2.0- to 3.9-foot class plantations and indicates slightly higher degrees of defoliation than in the foregoing class. Defoliation of 33 percent occurred at the 10 percent infestation level and 57 and 73 percent defoliation at the 50 and 75 percent infestation levels respectively. These increases in the amount of defoliation were to be expected since the 2.0- to 3.9-foot class trees had less foliage than trees in the 4.0- to 6.9-foot class.

In the past, control spraying operations have been initiated when 10 percent of the pines were infested with sawfly larvae in plantations averaging 6 feet and under and when plantations 7 feet and over were 20 percent infested. In consideration of shortleaf pine's remarkable ability to recover from severe defoliation, it would be advisable to revise these levels.

The opportunity to continue this approach to high population studies with a study of the number of colonies per tree at various infestation levels and a study of the defoliation of trees of specific heights by given numbers of larval colonies was not available on the Shawnee National Forest due to the pressure of control and survey activities. It should be noted, however, that practical application of these infestation-defoliation data can be made in predicting defoliation in shortleaf pine plantations at various red-headed pine sawfly population levels.



GRAPH 1. RELATIONSHIP BETWEEN PERCENT OF SHORTLEAF PINE TREES INFESTED WITH RED-HEADED PINE SAWFLY AND PERCENT DEFOLIATION (4.0 TO 6.9 FOOT HEIGHT CLASS).



GRAPH 2. RELATIONSHIP BETWEEN PERCENT OF SHORTLEAF PINE TREES INFESTED WITH RED-HEADED PINE SAWFLY AND PERCENT DEFOLIATION (2.0 TO 3.9 FOOT HEIGHT CLASS).

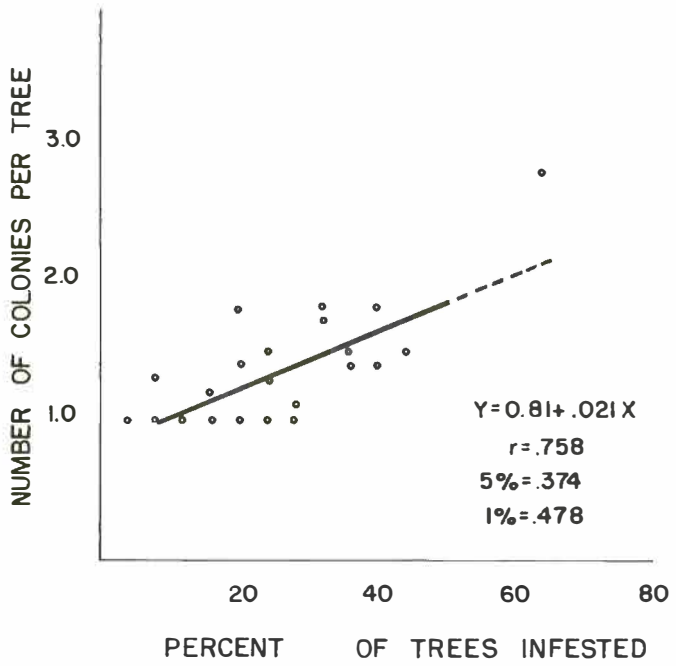
Infestation vs. Number of Colonies per Tree

A preliminary study of the infestation-defoliation relationship in the jack pine plantations was made on the Manistee National Forest in 1948. In these studies the number of colonies per tree at various infestation levels was determined. No attempt was made to classify the trees according to height class. Table 22, a summary of the data collected on the 30 plots of 25 trees per plot, indicates that the number of trees infested with more than a single colony of larvae increased as the percent of trees infested increased. For example, in the 1 to 9 percent infestation class, 0.8 percent of the trees were attacked by 2 colonies per tree while no trees were attacked by more than 2 colonies. In the 20 to 29 percent class, 3.6 percent of the trees had 2 colonies per tree and 0.7 and 0.4 percent of the trees had 3 and 4 colonies respectively. In the 60 to 69 percent class, 20.0 percent of the trees had 2 colonies, 12.0 percent and 8.0 percent of the trees had 3 and 4 colonies respectively, and 4.0 percent of the trees had 8 colonies.

TABLE 22. PERCENT OF TREES UNDER MULTIPLE COLONY ATTACK AT VARIOUS INFESTATION LEVELS IN JACK PINE PLANTATIONS MANISTEE NATIONAL FOREST - 1948

Number of Colonies per Tree:	(Percent Infestation classes) 1 - 9	10 - 19	20 - 29	30 - 39	40 - 49	50 - 59	60 - 69
	(Percent of trees infested)						
1	6.4	14.7	17.5	19.0	25.0		16.0
2	0.8	1.3	3.6	9.0	11.0		20.0
3			0.7	4.0	4.0		12.0
4			0.4	1.0	1.0		8.0
5				1.0			-
6							4.0
7							-
8							4.0

The average number of colonies per infested tree on the foregoing 30 plots was calculated and plotted in Graph 3. Coefficient of Correlation analysis indicated a significant relationship between the number of colonies and the percent infestation. The average number of colonies increased from 1.0 colony per tree at the 10 percent level to an average of 2.0 colonies per tree at the 60 percent level. How high this average figure could rise cannot be predicted from these limited data. However, it would appear that as the infestation neared the 100 percent level the determining factor would be the size of the tree and foliage available for oviposition. Further studies of this type were not possible as the sawfly population on the Manistee National Forest was markedly reduced through aerial control applications and the population did not recover in 1949.



GRAPH 3. RELATIONSHIP BETWEEN PERCENT OF JACK PINE TREES INFESTED WITH RED-HEADED PINE SAWFLY LARVAE AND THE AVERAGE NUMBER OF COLONIES PER TREE.

Number of Colonies per Tree vs. Defoliation

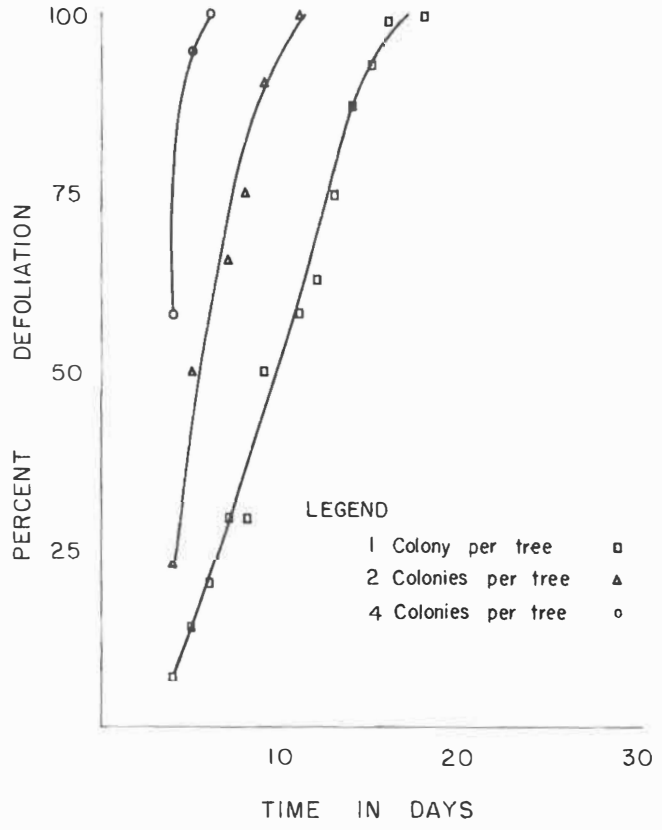
During the 1949 field season red-headed pine sawfly colonies were artificially introduced on both red and jack pine trees in an attempt to resolve the problem of feeding intensities at various colony levels. In these studies 1, 2, 4, and 8 second instar colonies were placed on 1, 2, 4, and 6-foot red and jack pine trees. Three replicates of comparable trees were selected for these studies. Observations were made of the number of colonies, the intensity of defoliation, the instar, and the rate of defoliation. As the trees were stripped, larval migration and mortality data were taken; this aspect of the study was discussed in a previous section of this paper. Unfortunately, a disease caused high larval mortality during the latter part of the defoliation studies and markedly influenced the intensity of larval feeding. General trends can be shown, however, and these will be presented.

The defoliation trends on the red pine plots were more pronounced than the trends on the jack pine plantations. Also, the disease appeared slightly later on the red pine plots. For these reasons defoliation trends on the red pine plots will be discussed first and will be followed by a discussion of the jack pine.

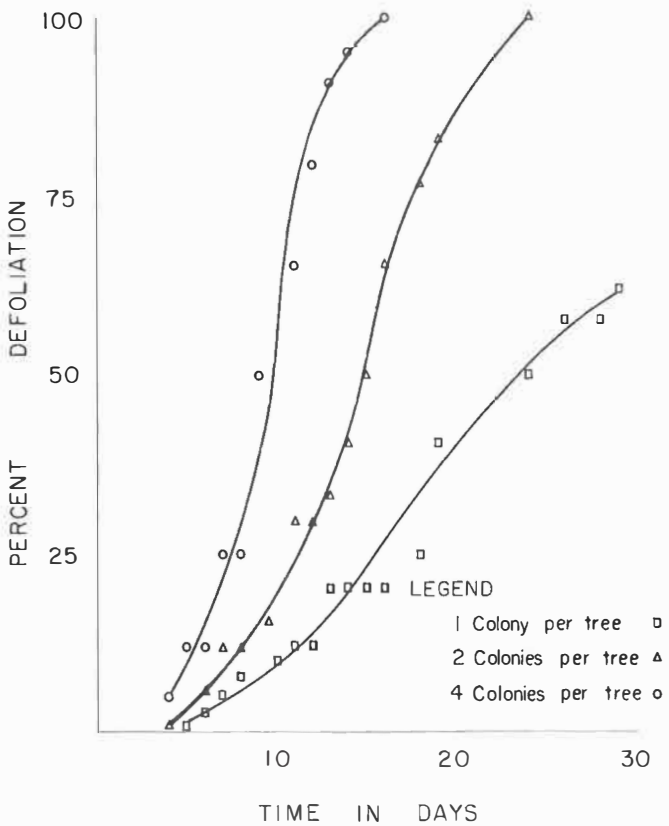
(Red Pine)

Red pine experimental plots selected for the defoliation studies were located in sandblow areas. Trees in these sandblows are susceptible to sawfly attack and represent a large proportion of the Manistee National Forest sites under current sawfly attack. On the 1-foot red pine plots, 4 colonies per tree completely defoliated the pines by the end of the 6th day (Graph 4). Two colonies per tree caused complete defoliation by the 11th day and 1 colony by the 18th day. On the 2-foot red pine plots, complete defoliation was accomplished by 4 and 2 colonies per tree by the 10th and 22nd day respectively, as illustrated by Graph 5. One colony defoliation which reached the 50 percent level by the 25th day was apparently influenced by the larval disease. Disease also interrupted feeding on the 4- and 6-foot plots around the 19th day. Data collected on these plots indicate that the same general defoliation trends appear to be followed by these sawfly populations with defoliation progressing at a slower rate.

In addition to defoliating the initial host tree, introduced larvae left the stripped host tree and many established themselves on adjacent pines where they continued to feed voraciously. Table 8 lists the adjacent 1-foot red pines attacked by the migrating larvae and the intensity of defoliation injury. Of the 29 trees attacked by migrants from the 3-4 colony host tree, 12 suffered defoliation in excess of 50 percent; 8 of the trees were completely stripped. Migrants from the 2-colony trees established themselves on 13 adjacent trees. Six of these trees suffered defoliation in excess of 50 percent, two of them being completely defoliated. One colony tree migrants reached 5 adjacent trees where they caused but minor defoliation injury.



GRAPH 4. RATE OF DEFOLIATION OF ONE-FOOT RED PINE BY ONE, TWO AND FOUR RED-HEADED PINE SAWFLY COLONIES.



GRAPH 5. RATE OF DEFOLIATION OF TWO-FOOT RED PINE BY ONE, TWO, AND FOUR RED-HEADED PINE SAW-FLY COLONIES.

Migrant larvae from sod-growing 2-foot red pine trees also continued to feed after leaving their host and establishing themselves on adjacent host trees. Table 9 lists the trees attacked by larvae from the 4-colony trees and shows that 14 trees were infested; two of the trees were completely stripped of their foliage. One tree of the ten trees infested by 2-colony tree migrants was 50 percent stripped.

(Jack Pine)

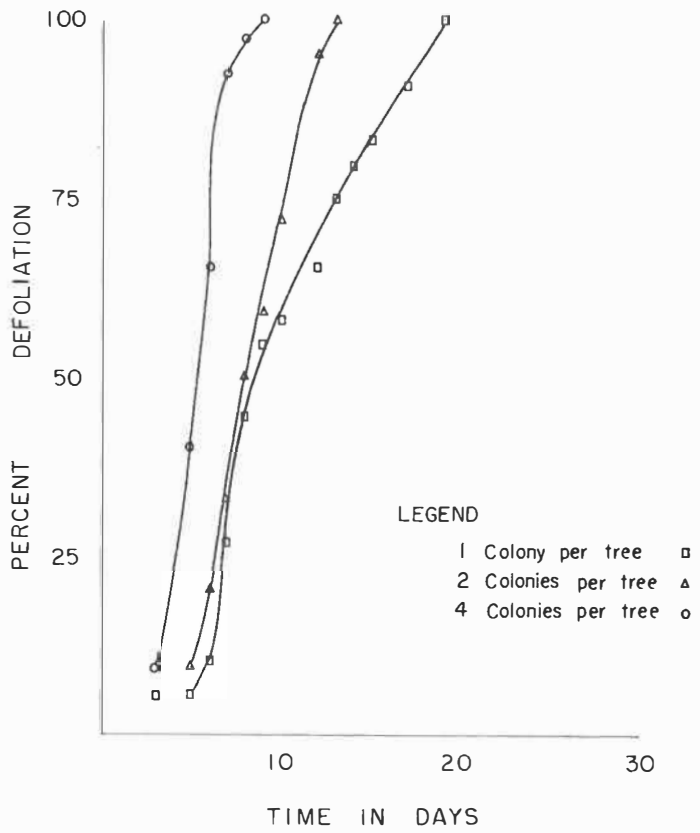
The jack pine plots were also located on the sandblow areas as these plantations represent some of the most susceptible forest plantings on the Manistee National Forest. On these 1-foot plots complete defoliation was accomplished by 1, 2, and 4 colonies within an average of 19, 13, and 9 days respectively (Graph 6). Although disease curtailed larval feeding on the 2, 4, and 6-foot plots, the general trends on the red pine plots were followed up to the time of interrupted feeding. Larval migrants from the sandblow growing 1-foot jack pines suffered rather high mortality after leaving their host trees, due to high sand temperatures. Larvae from the 4-colony trees attacked 21 nearby pines causing defoliation in excess of 50 percent on 4 trees. Migrants from the 2-colony trees attacked 28 trees, 3 being completely stripped and 2 losing 50 percent of their foliage. One-colony migrants established themselves in 23 trees, completely defoliating one tree and severely injuring 2 others.

Practical application of these defoliation intensity data will be found in predicting the rate of defoliation on forest plantations and the time limits within which control operations will have to be completed to avoid serious defoliations. For example, control applications against the red-headed pine sawfly must be completed within 10 days to prevent 50 percent defoliation of 1-foot red pine trees by 1-colony per tree infestations and by the 5th day to prevent 50 percent defoliation by 2-colony infestations. To avoid complete stripping of 1-foot red pine, control must be applied before the 18th day on 1-colony infestations and by the 11th and 6th day on 2- and 4-colony infestations. On the 1-foot jack pine plantations, 50 percent defoliation would result by the 9th day on 1 colony infestations, by the 7th and 6th day from 2- and 4-colony attacks.

Site Preference

It should be emphasized that outbreak populations of insects often so obscure the host-insect relationships that little information can be obtained concerning the ecological site or host preferences of the species in question. Generally, it is not until endemic conditions return that a well-rounded ecological picture can be obtained. This was true in regard to the red-headed pine sawfly although some insight into the ecology was possible during the outbreak status.

During the 1945-1947 sawfly outbreaks on the Ottawa and Manistee National Forests a few areas of shortleaf pine, red, and jack pine, which sustained exceedingly severe defoliation, were encountered. These areas, kept under surveillance during the decline in the sawfly population and also during the endemic period which followed, have



GRAPH 6. RATE OF DEFOLIATION OF ONE-FOOT JACK PINE BY ONE, TWO, AND FOUR RED-HEADED PINE SAW-FLY COLONIES.

greatly clarified ideas on sawfly site preference on these two National Forests. For the sake of clarity, the ecology of the insect on the two National Forest areas will be discussed separately.

(Shawnee National Forest)

Defoliation. During the early phases of the red-headed pine sawfly investigations on the Shawnee National Forest, heavy sawfly defoliation was observed in the shaded parts of many shortleaf pine plantations. In light of the comments of Brown and Davidulf (1942) and Atwood and Peck (1943) that the red-headed pine sawfly was a "sun loving" species; the suggestion that shaded areas were relatively free from red-headed pine sawfly attack (MacAloney and Secrest - 1944); and Beal's (1942) comments that pines growing in the open were less subject to attack by the sawfly than shaded pines; the advisability of recommending the underplanting of hardwood stands with hard pines as followed in the past was open to serious question.

A possible solution of this paradox was sought through comparing the number of sawfly infested open-growing shortleaf pines with the number of infested pines growing in shaded areas of the same plantation. In approaching this problem, only the number of trees attacked was considered. Obviously, the degree of defoliation would bear little weight in the problem of preference. Although pines shaded or suppressed by hardwoods have much less foliage than open-growing pines and hence would be stripped of their foliage much more rapidly than the open-growing pines, this does not have great bearing on the selection question.

Observations on the Shawnee National Forest indicated that red-headed pine sawfly infestations were the heaviest and the defoliation most severe on shaded shortleaf pines when both shaded and open-growing pines were present in the same plantation. Generally, when open-growing pines were infested to any degree, all of the nearby over-topped pines were infested. As the sawfly population decreased on this Forest in 1947 and 1948, open portions of the plantations were the first to become free of sawfly activity. In areas where red-headed pine sawfly activity was negligible in open plantations, eggs were located only on pines growing in the shade of over-topping scattered hardwoods. During the egg parasite surveys in 1948 and 1949, discussed in a foregoing section, sawfly activity was observed only in the shaded sites although the open sites were searched quite thoroughly. These findings appear to corroborate Beal's (1942) viewpoint that the red-headed pine sawfly is a shade preferring species. Beal found 23 percent of the open-growing pines infested as compared to 33 percent of the over-topped shaded pines.

Red-headed pine sawfly larvae feeding as a colony appear to seek out the more exposed portions of the tree, as has been pointed out in a foregoing section. After the first or second instar they feed primarily from the tips of the branches and leader toward the base of the tree. Since larval colonies seldom migrate from their feeding site on any particular tree to another tree unless the first tree has become completely defoliated, it is apparent that the site selection is primarily that of the female adult sawfly. The fact that larval colonies are generally observed feeding on the more exposed portions of the pine trees has led many to consider the red-headed pine sawfly a sun-loving species.

Since the female sawfly initially determines where the larval feeding will take place, her selection governs almost completely the type of tree attacked. Therefore, major consideration was given to egg presence and location rather than to larval presence to resolve the problem. Furthermore, by employing the presence of sawfly eggs as the site selection criterion, the complicating factor of larval absence due entirely to heavy egg parasitism was avoided.

Egg Site Selection. In the foregoing sections, it has been pointed out that the red-headed pine sawfly seemed to prefer shaded pine trees when offered a choice. Also, when the sawfly population declined to endemic status, the majority of the sawfly eggs were found in the shaded portions of the plantations. In addition to these sites, plantation edges, wide spaced plantings, and non-closed plantations under heavy attack were examined to further resolve the problem of egg site selection.

In the non-shaded plantations the concentration of sawfly defoliation was observed along the edges of the stand. In border pines the branches extended to the ground and thus produced densely shaded needles. Examination of these borders revealed that the concentration of sawfly eggs was laid on the lower branches well back in the dense needle clusters. In many plantations, severe defoliation was observed only in localized areas of poor survival where low crowned, lone trees predominated. When these lone trees were attacked, the concentration of eggs was laid on the lower branches well back in the dense needle clusters in the shade. Figure 26 illustrates this type of plantation and, in the foreground, one of the heavily attacked shortleaf pine trees.

During the sawfly outbreak in 1947, data were assembled concerning the egg sites selected by ovipositing female sawflies in two open plantations. Egg batches on 20 open-growing trees were tallied during the second generation and on 10 trees during the third generation. Forty-three of the 70 egg batches were laid on the south and east side of the trees, 9 were laid on the north and 6 on the west side and 12 on the leader. All (58) of the egg batches were laid on the under side of the branches well back in the dense needle clusters with the exception of the 12 egg batches laid on the leaders. Apparent contradictory evidence of roadside and recreational site pines being attacked by the sawfly may be explained as a simple matter of availability. Presented with one choice, the sawfly will oviposite on whatever species of hard pine happens to be suitable and available regardless of the site.

In shaded plantations, egg site selection by ovipositing females was not observed to follow any specific pattern. Eggs appeared to be laid indiscriminately on all portions of the tree. Female sawflies were, however, observed to oviposite in the most dense portions of partially shaded trees in a few instances.

In summary, the red-headed pine sawfly appeared to be a shade preferring species on the Shawnee National Forest. Under epidemic conditions, heavy concentrations of sawfly larvae were often found in open-growing, as well as in shaded, plantations. However, under endemic conditions, the sawfly activity was generally confined to the shaded portions of the pine plantations and to lone, densely crowned, open-growing trees.

FIGURE 26. OPEN-GROWING SHORTLEAF PINE PLANTATIONS HIGHLY SUSCEPTIBLE TO RED-HEADED PINE SAWFLY ATTACK. PINE IN FOREGROUND WITH HEAVY CONCENTRATION OF SAWFLY EGGS ON LOWER BRANCHES IN DENSE NEEDLE CLUSTERS.

(Manistee National Forest)

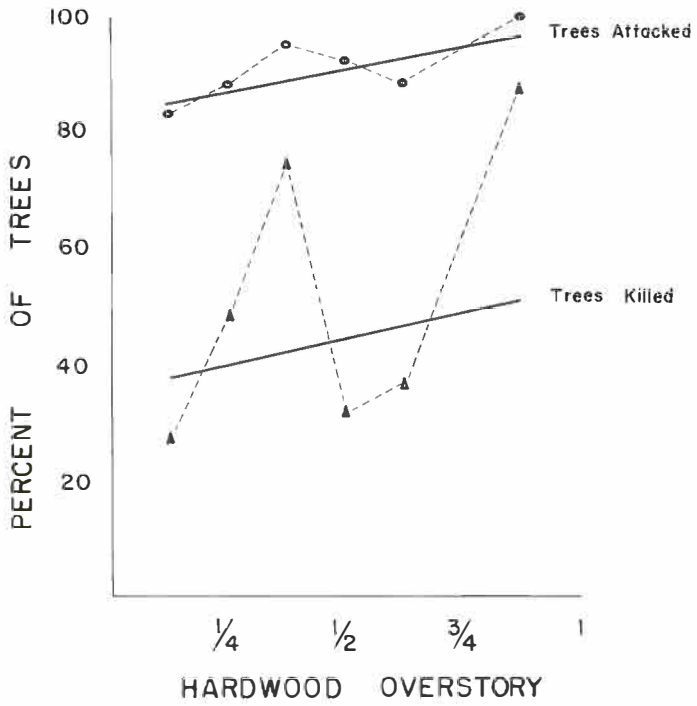
The relationship between heavy red-headed pine sawfly concentrations and shaded pine plantations was also found on the red and jack pine plantations on the Manistee National Forest. During the 1946-1948 outbreak heavy defoliation was observed primarily on the following three red and jack pine plantation sites: plantations under heavy hardwood overstories, plantation edges, and plantations in sandblows.

Shaded Plantations. Severe defoliation resulting from the 1946-1948 red-headed pine sawfly outbreak was encountered on several thousand acres of jack pine plantation on the Manistee Ranger District of the Manistee National Forest. This infestation was more severe, both from the standpoint of number of trees attack and the degree of defoliation on the plantations growing under complete and partial shade than on open plantations. H. G. Fox and R. P. Dahl, summer employees of the Milwaukee Forest Insect Laboratory, conducted a survey of these shaded jack pine plantations to evaluate the influence of cover on the number of trees injured and killed. In this survey, the degree of hardwood cover was roughly estimated on the basis of the amount of sky covered. One-eighth sky cover categories were used. The number of jack pines killed and those partially defoliated but not killed in 1946 and 1947 were tallied, together with the number of non-injured trees. Table 23 is a summary of the defoliation data collected on the 25 1/10th-acre plots examined during this 560-acre survey. Coefficient of Correlation analysis of these data indicated that no significant relationship existed between the number of trees killed or injured and the amount of hardwood cover. Possible explanation for the lack of significance may be found in the severity or intensity of the outbreak. On these plots, 1,239 of the 1,459 trees were attacked, representing an 88.3 percent infestation. Possibly under less severe conditions, the relationship might have been more pronounced.

Although the relationship was not significant, a straight line was fitted through the data using the Coefficient of Correlation method, to illustrate the mild increase in both the number of trees attacked and the number of trees killed at various cover levels. Graph 7 shows the gradual increase in both tree injury and tree mortality as the amount of tree cover increased.

TABLE 23. RELATIONSHIP BETWEEN HARDWOOD COVER AND NUMBER OF JACK PINE TREES ATTACKED BY RED-HEADED PINE SAWFLY MANISTEE NATIONAL FOREST - 1948

Cover	Total Trees Injured		Total Trees Killed		Total Non-Infested		Basis
	Number	Percent	Number	Percent	Number	Percent	
1/8	381	83	123	27	80	17	461
1/4	203	88	111	48	27	12	230
3/8	181	95	141	74	10	5	191
1/2	183	92	63	32	17	8	200
5/8	274	88	116	37	36	12	310
3/4							
7/8	67	100	58	87	0	0	67
Total	1,289	88.3	612	42.0	170	11.7	1,459



GRAPH 7. RELATIONSHIP BETWEEN HARDWOOD OVERSTORY AND PERCENTAGE OF JACK PINE TREES ATTACKED BY RED-HEADED PINE SAWFLY.

After the 1948 defoliation was completed on the Manistee Ranger District, the writer cruised one 80-acre jack pine plantation growing under an oak overstory to evaluate the accumulative 1946-1948 sawfly injury. Nine plots of 25 trees each were examined along a two-tree strip through the plantation. Presence or absence of an overstory was noted, but no attempt was made to evaluate the cover. In the covered portions of the plantation, 98.4 percent of the 123 jack pines had been attacked as compared to 75.7 percent of the 111 open-growing jack pines. Among the pines growing under cover, 74.8 percent were dead as compared to 22.5 percent among the open-growing pines.

During the 1949 season, sawfly activity was very low on these plantations. The sawfly larvae observed were feeding on the few shaded jack pines remaining in the understory areas. None of the open-growing trees were found to be attacked except where all of the shaded pines had been killed through defoliation.

Plantation Edges. Numerous comments have been made concerning the heavy initial sawfly attack along the boundaries of closed jack pine plantations. This characteristic attack pattern has been observed on both the Manistee and on the Shawnee National Forests, as well as on forest plantations throughout the Lake States Region. Cursory examination of these plantation edges revealed that the branches of the jack pines extend to the ground. Also, it was noted that the foliage on these trees was more dense than on the trees growing within the closed plantation. The majority of the sawfly eggs observed along these borders during low population activities in 1948 and 1949, on the Cadillac Ranger District, were on the protected needles well under the lower branches and near the ground. As was to be expected, defoliation was also more severe along these plantation edges than within the closed stands.

Border Hardwoods. During the 1946-47 sawfly outbreak on the Cadillac Ranger District, exceedingly heavy defoliation was found along the edges of the jack pine plantations where the crowns of bordering hardwoods extended over the pines. So severe was this defoliation that the majority of the over-topped and adjacent trees were completely stripped of their foliage. Three representative jack pine plantations were selected for further investigation of this border-hardwood preference. One south boundary and two east boundaries where border hardwoods shaded the outer rows of jack pine were examined and charted. The distance of each tree was measured from an established base line, tree height was estimated to the nearest foot, and the percent defoliation was estimated using the geometric progression procedure outlined in a foregoing section. The hardwood stem and crown was located and plotted as a crown projection on the plantation diagram. Sawfly defoliation was identified by the presence of bark feeding, needle sheath or fragment remains, and by the presence of large quantities of larval frass.

Figures 27 and 29 illustrate the heavy kill associated with the hardwood crown on the south boundary of the jack pine plantation. Figures 28, 30, and 31 illustrate the heavy kill encountered along the east border. The decrease in feeding intensity may possibly be explained on the basis of differential amounts of foliage on the shaded as compared to the open-growing trees. The striking decline in the number of trees

FIGURE 27. HEAVY RED-HEADED PINE SAWFLY INFESTATION ASSOCIATED WITH SOUTH BORDER OF JACK PINE PLANTATION SHADED BY RESIDUAL HARDWOODS.

FIGURE 28. HEAVY RED-HEADED PINE SAWFLY INFESTATION ASSOCIATED WITH EAST BORDER OF JACK PINE PLANTATION SHADED BY RESIDUAL HARDWOODS.

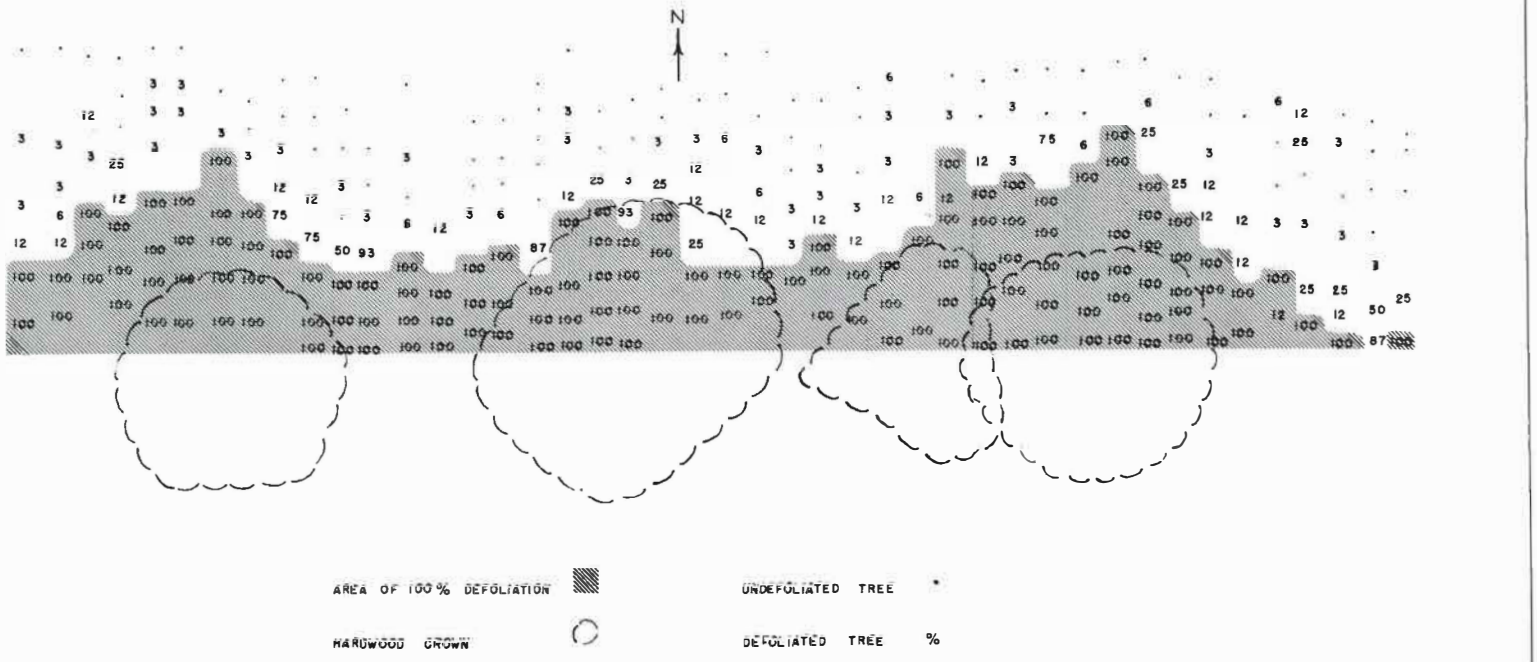


FIGURE 29. DIAGRAM OF SOUTH EDGE OF JACK PINE PLANTATION ILLUSTRATING HEAVY RED-HEADED PINE SAWFLY ATTACK IN VICINITY OF HARDWOOD CROWNS.

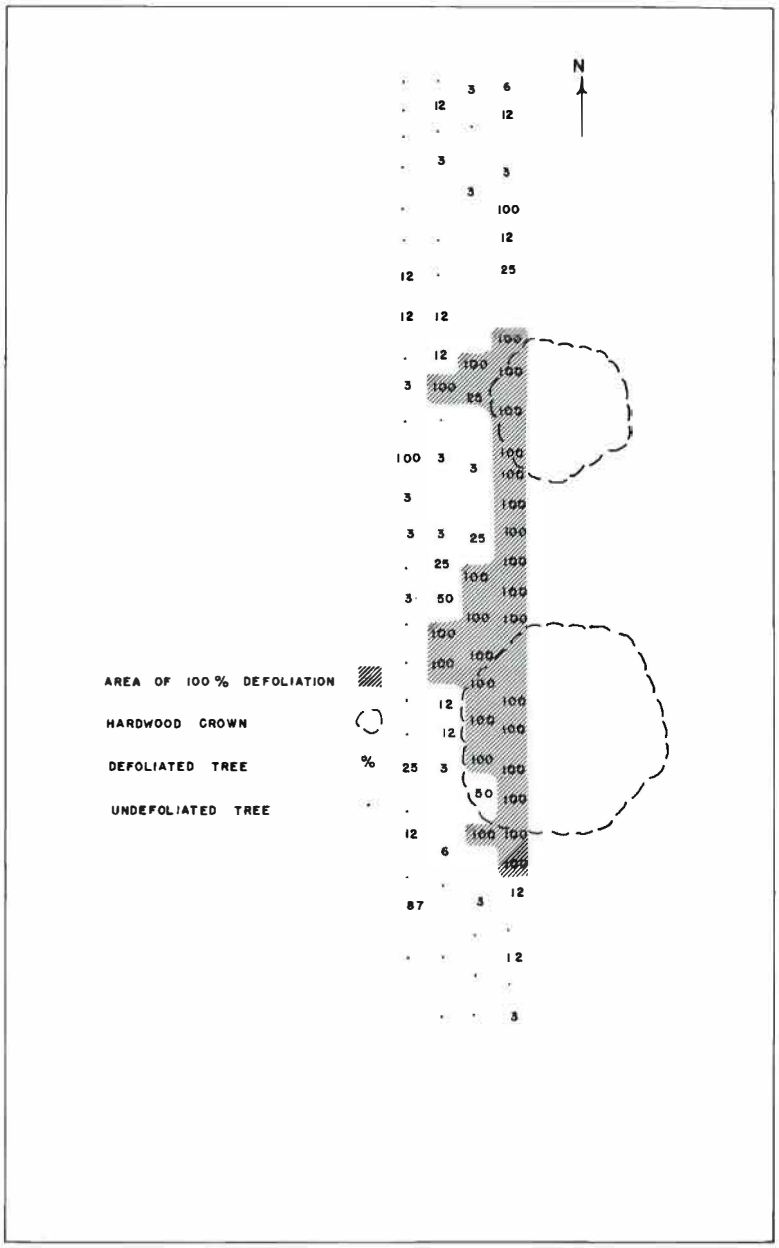


FIGURE 30. DIAGRAM OF EAST EDGE OF JACK PINE PLANTATION ILLUSTRATING HEAVY RED-HEADED PINE SAWFLY ATTACK IN VICINITY OF HARDWOOD CROWNS.

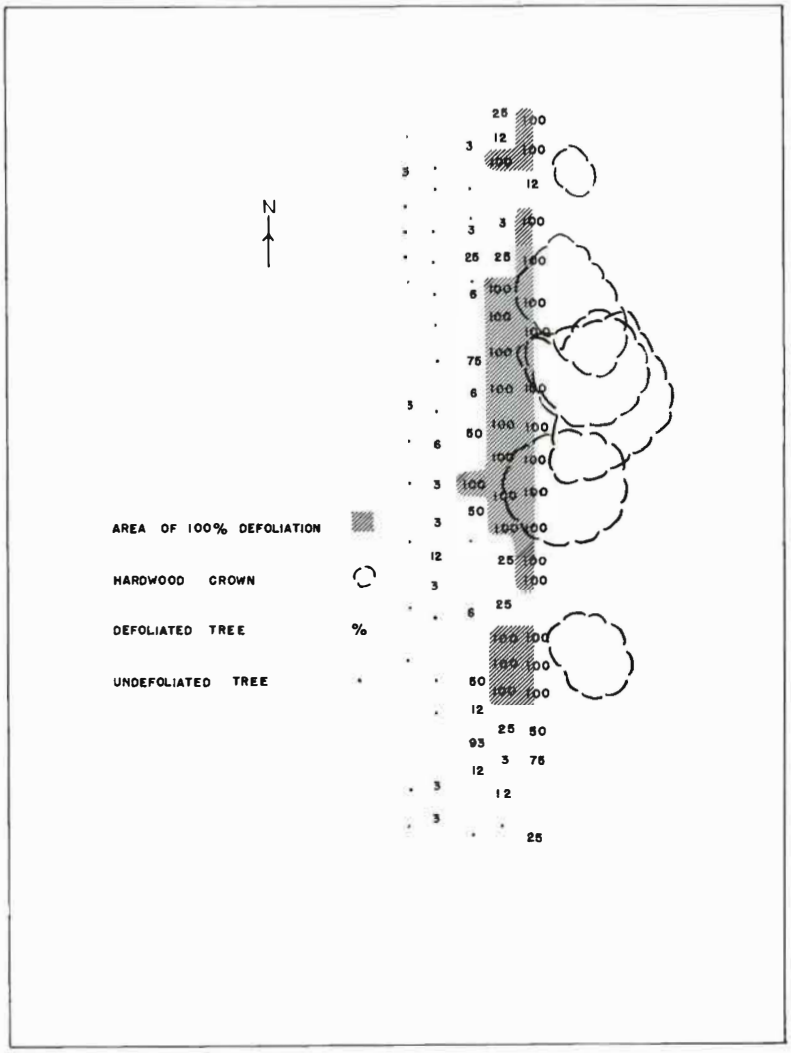


FIGURE 31. DIAGRAM OF EAST EDGE OF JACK PINE PLANTATION ILLUSTRATING HEAVY RED-HEADED PINE SAWFLY ATTACK IN VICINITY OF HARDWOOD CROWNS.

attacked as the distance from the hardwood crowns increased cannot be explained on this basis. It appears to be most closely related to the reduced influence of the hardwood crown as the distance increases.

Central Hardwood Influence. Three jack pine plantations which had single over-topping hardwoods within the plantation were selected in which to study the apparent shade preference in the absence of the border effect. When these areas were planted, jack pine seedlings were spaced in 6 x 6 foot rows from one boundary to the other. The areas directly under the residual hardwoods were also planted at this time. Plots which surrounded these central hardwoods and several rows of adjacent jack pines were selected and the distance of the hardwood and of each pine from an established base line determined. The height and percentage defoliation of each pine was estimated. Hardwood crown projections were superimposed over the plotting of the jack pine-hardwood area.

The intensity of sawfly attack was most closely associated with the presence of the hardwood crowns. This relationship, somewhat obscure in Figure 32 due to the heavy attack, is striking in Figures 33, 34, and 35 (plottings of Figures 36, 37, and 38). Trees directly under the hardwood crown and also in a band extending to the north of the crown were completely defoliated. The number of trees attacked, actually the crux of the problem, declined drastically as the distance from the crown increased. In view of the long extension of the area of heavy sawfly attack to the north and its relatively short extension to the south, it would appear that some factor or factors associated with light governed the selection of these particular sites for oviposition.

Sandblows. In addition to the foregoing pine plantation sites, in which jack pine trees growing under an overstory or under single hardwoods were seriously attacked by the red-headed pine sawfly, sandblow plantings were also found to be very susceptible to sawfly attack. Both jack and red pine sandblow plantations suffered heavy defoliation on the Cadillac Ranger District during 1946, 1947, and 1948. Sawfly defoliation, severe throughout the sandblow area of these plantations, rarely extended beyond the first or second row of pines growing in the sodded or closed portions of the stand. Figures 39 and 40 illustrate the sandblow jack and red pine plantation types attacked.

The majority of the sawfly egg batches laid on these red and jack pine sandblow plantings were deposited on the lower portions of the branches well back in the dense needle clusters. Often single pines within a sandblow group, which possessed densely shaded branches as compared to their neighbors, would have the major concentration of sawfly eggs laid on them. Figure 41 illustrates just such an example. The tree in the right foreground had four egg batches laid on it while the surrounding pines were free of eggs and larvae of the sawfly.

The initial red-headed pine sawfly attack of new plantings appeared to take place in isolated sandblows. A very striking example of this attack is presented in Figure 42. In this planting one year old red pines growing in the scattered sandblows were attacked while the pines in the sodded areas were not attacked. In Figure 43 the trees indicated with an "X" were attacked. This preference for pines in sandblows also

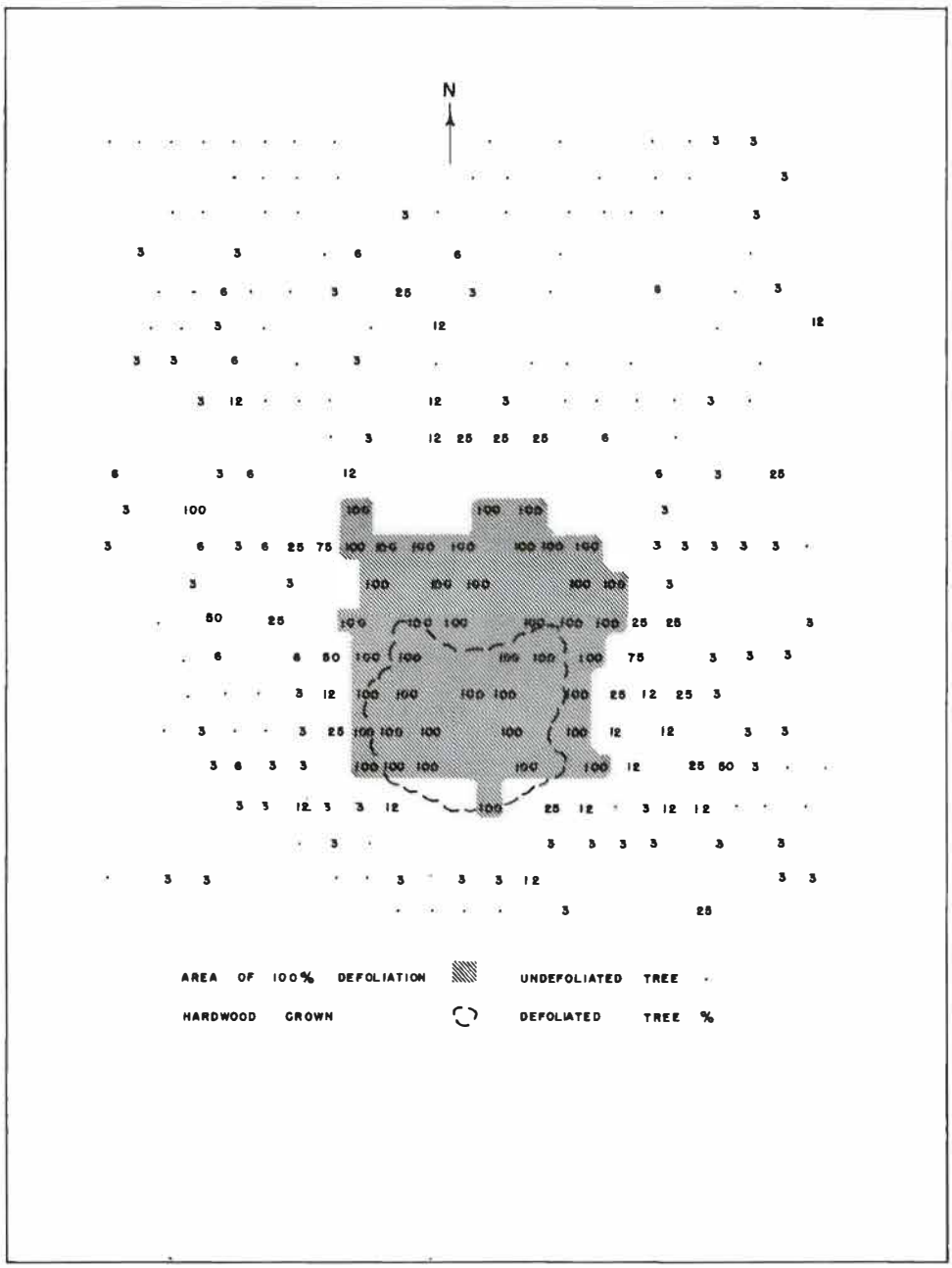


FIGURE 32. DIAGRAM OF JACK PINE PLANTATION ILLUSTRATING HEAVY SAWFLY ATTACK IN VICINITY OF HARDWOOD CROWN.

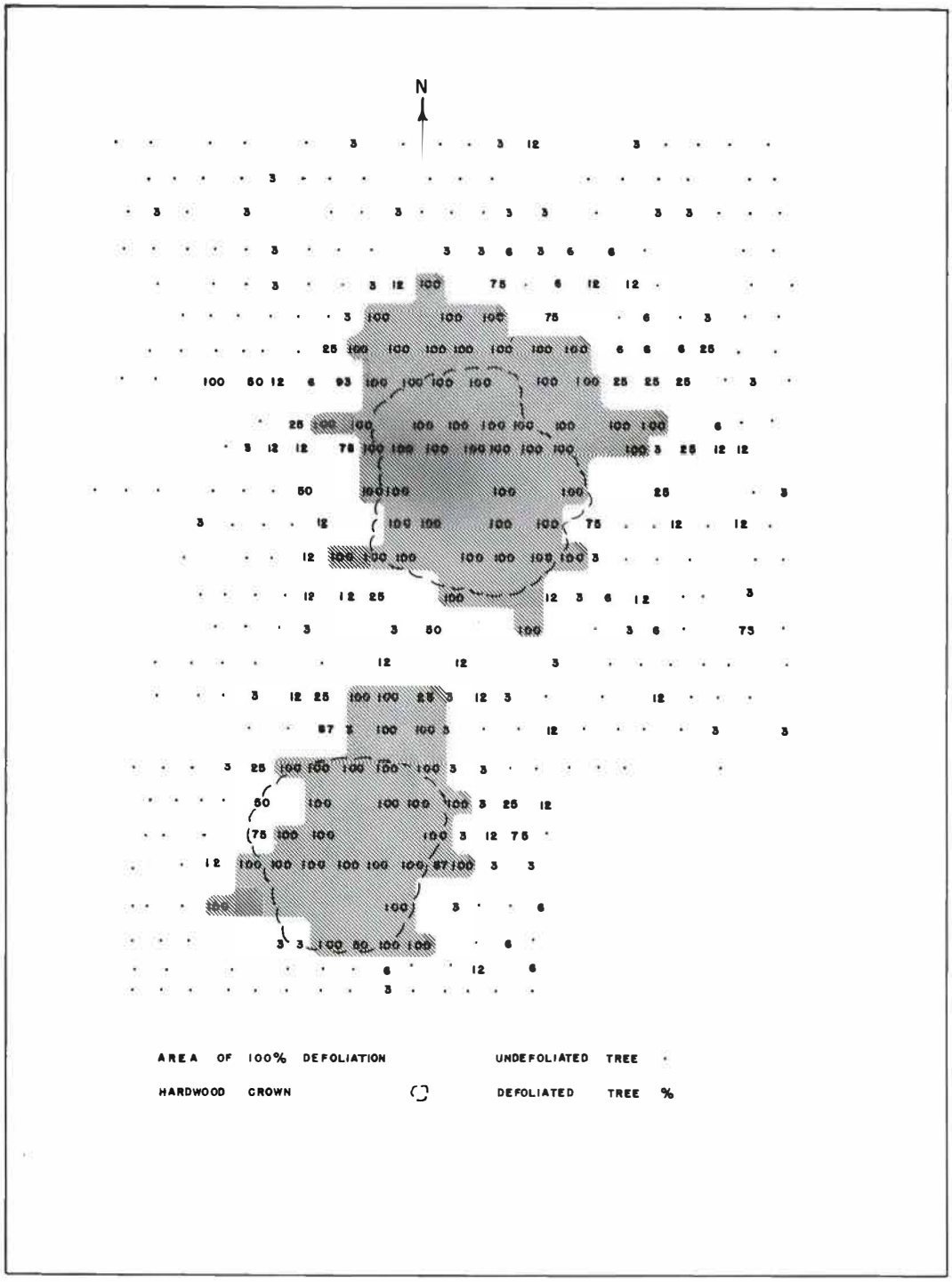


FIGURE 33. DIAGRAM OF JACK PINE PLANTATION ILLUSTRATING HEAVY SAWFLY ATTACK IN VICINITY OF HARDWOOD CROWNS.

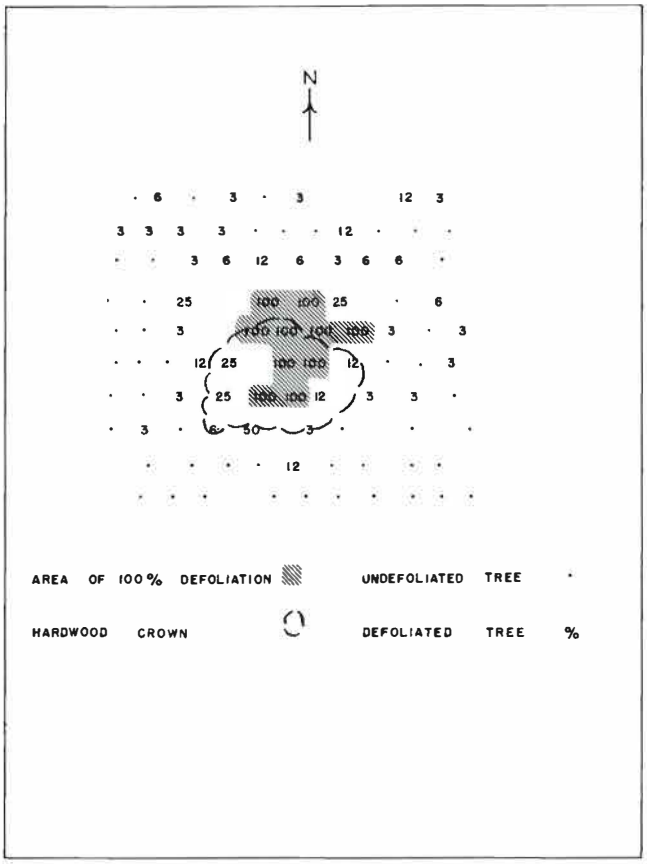


FIGURE 34. DIAGRAM OF JACK PINE PLANTATION ILLUSTRATING HEAVY RED-HEADED PINE SAWFLY ATTACK IN VICINITY OF HARDWOOD CROWN.

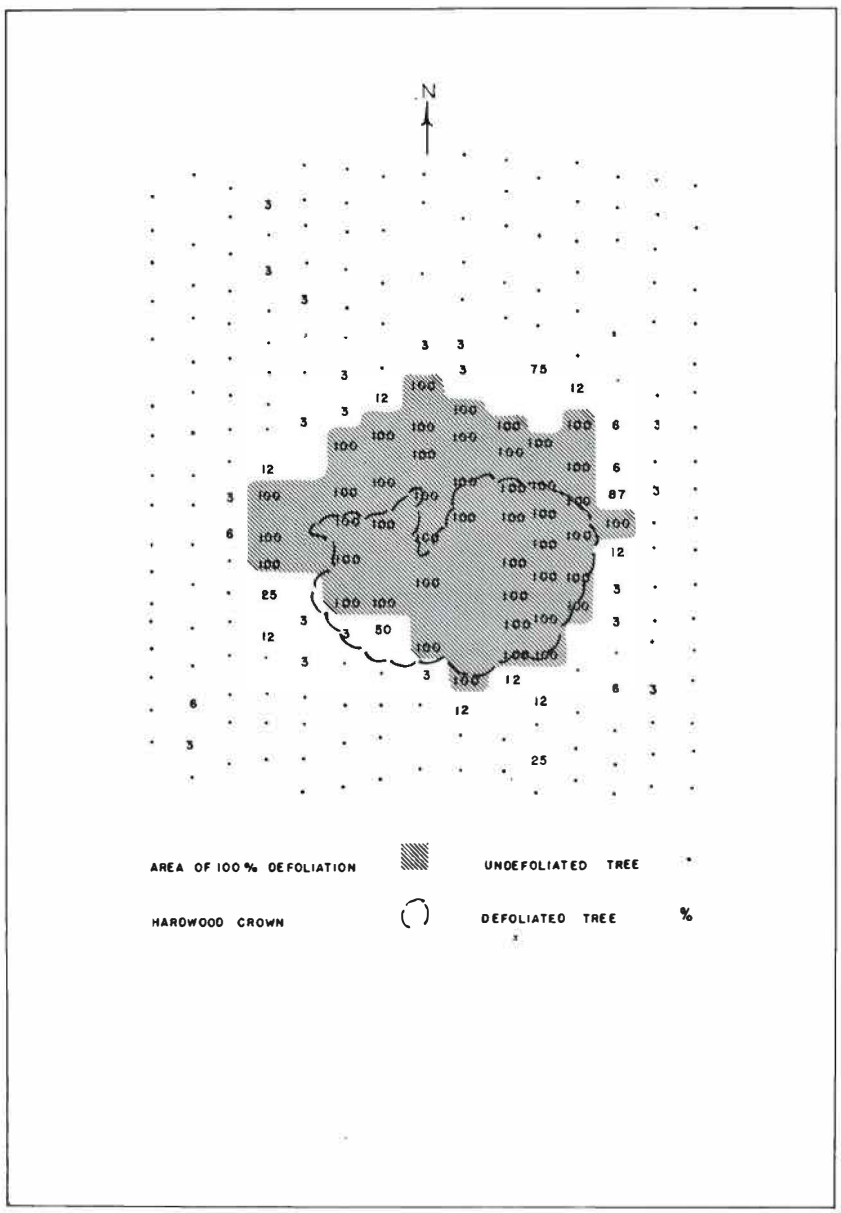


FIGURE 35. DIAGRAM OF JACK PINE PLANTATION ILLUSTRATING HEAVY RED-HEADED PINE SAWFLY ATTACK IN VICINITY OF HARDWOOD CROWN.

FIGURE 36. RESIDUAL HARDWOOD IN JACK PINE PLANTATION PLOTTED AS FIGURE 33.

FIGURE 37. RESIDUAL HARDWOOD IN JACK PINE PLANTATION PLOTTED AS FIGURE 35.

FIGURE 38. HEAVY RED-HEADED PINE SAWFLY INFESTATION AND KILL ASSOCIATED WITH RESIDUAL HARDWOOD CROWN WITHIN CLOSED JACK PINE PLANTATION.

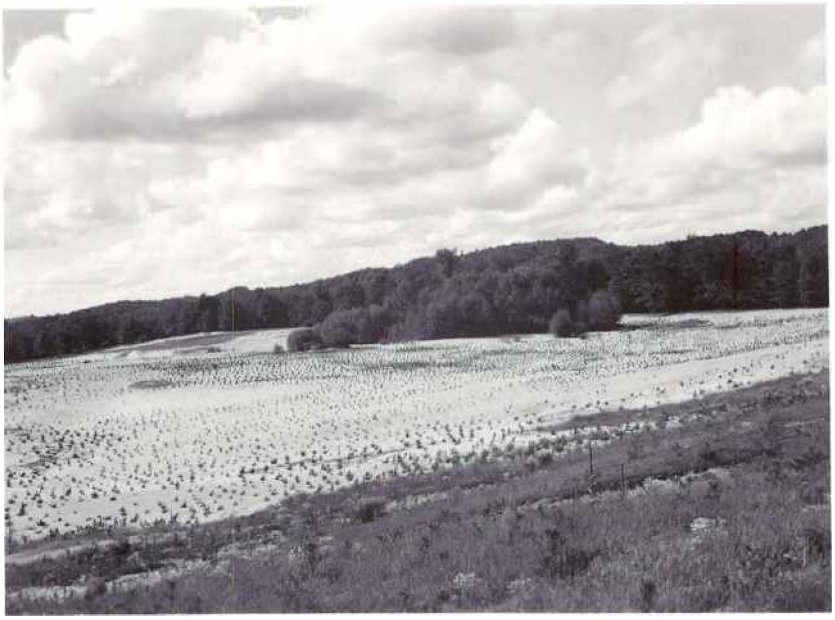


FIGURE 39. SANDBLOW JACK PINE PLANTATION HEAVILY ATTACKED BY RED-HEADED PINE SAWFLY. MANISTEE NATIONAL FOREST - 1948.

FIGURE 40. SANDBLOW RED PINE PLANTATION HEAVILY ATTACKED BY RED-HEADED PINE SAWFLY. MANISTEE NATIONAL FOREST - 1948.

FIGURE 41. RED PINE IN ISOLATED SANDBLOW. SINGLE TREE IN RIGHT FOREGROUND WITH FOUR EGG BATCHES. NOTE DENSE NEEDLE CLUSTERS CLOSE TO GROUND.

FIGURE 42. SANDBLOW RED PINE UNDER INITIAL RED-HEADED PINE SAWFLY ATTACK. PLOTTING OF THIS PLANTATION IN FIGURE 43.

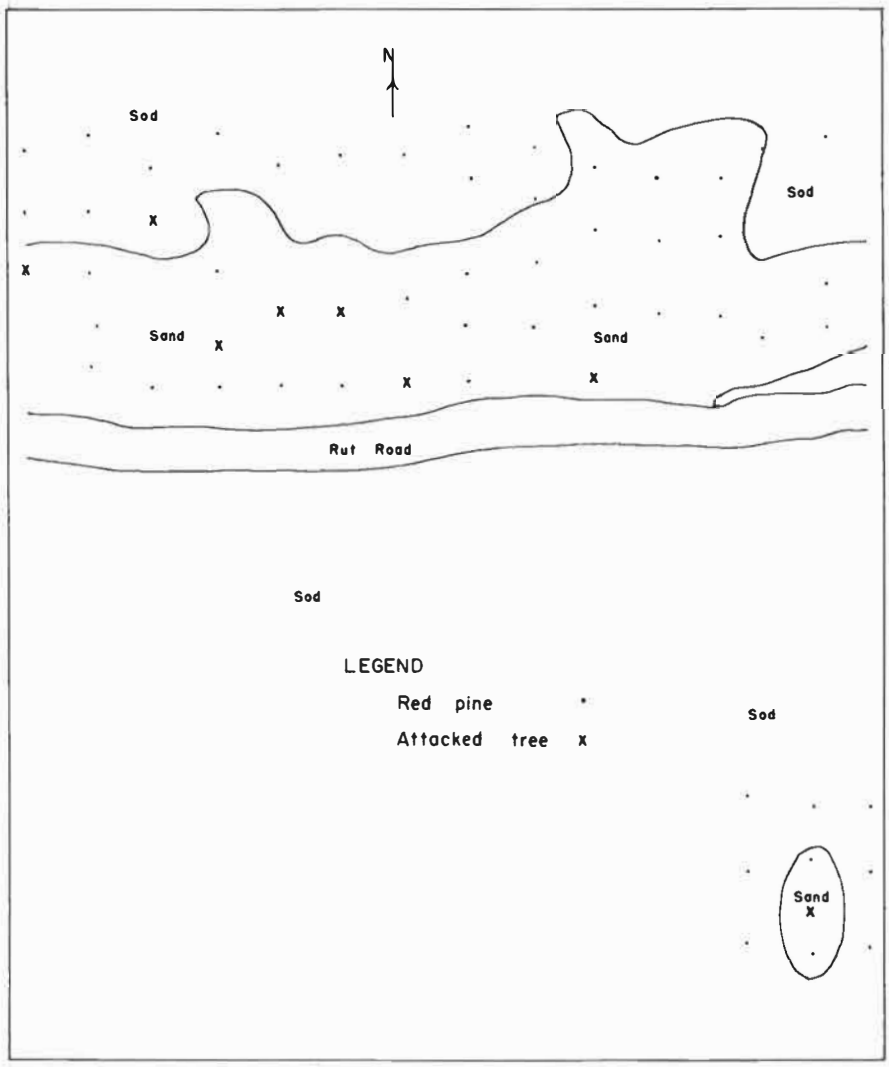


FIGURE 43. DIAGRAM OF RED PINE PLANTATION ILLUSTRATING INITIAL RED-HEADED PINE SAWFLY ATTACK IN ISOLATED SANDBLOWS.

took place in the older, widely-spaced, non-closed sandblow plantations. One such area of widely-spaced jack pine where survival was poor was observed in an otherwise closed and free from attack site. These open-growing pines with branches extending to the ground presented densely shaded egg sites which invariably were selected. A sample plot 450 feet long by 50 feet wide was taken through the center of this sandblow area. Figure 44 illustrates the severity of the infestation and the seriousness of the attack on part of this plot.

In the foregoing discussion the site preference of the red-headed pine sawfly and its activities under outbreak status were examined. Sawfly attack, both from the standpoint of number of trees attacked and the seriousness of defoliation, was closely associated with the presence of over-topping hardwood cover. Severe attack was also observed on open-growing, widely-spaced trees located in sandblows and on plantation edges. Red-headed pine sawfly eggs were most numerous in pines in the shaded portion of the stand, and on the shaded portions of the trees growing in the open.

Low Population Investigations (Population Reservoirs)

The need for investigations of the ecology of low density insect populations has been mentioned in a foregoing section of this paper. Although the key to the survival of the species and to the successful predicting of insect outbreaks possibly lies in an understanding of low population activities, few comprehensive studies of insect population reservoirs have been made. Hodson (1941) and Rees et al (1947) have published two of the few papers containing information on this problem; the former on the forest tent caterpillar and the latter on gypsy moth population studies.

Throughout the foregoing discussions concerning sites selected during epidemic conditions on the Shawnee and Manistee National Forests, the high percent of infestation and the seriousness of the subsequent defoliation in shaded, edge, and sandblow areas has been emphasized. These areas of most severe injury were observed periodically during the endemic period following the recent sawfly outbreaks to determine whether they would maintain their differential infestations. Practically every susceptible pine site examined maintained a reservoir population long after less susceptible areas became free of sawfly activity. These population reservoirs could conceivably be the loci of future outbreaks. In the following discussion the reservoir sites on the Shawnee and Manistee National Forests are discussed separately as they represent two different geographic areas with different host species.

Shawnee National Forest

(Shaded Plantations)

During the red-headed pine sawfly population decline on the Shawnee National Forest in 1945, open plantation areas were the first to become free of sawfly activity. High populations continued for several generations on the shaded portions of these plantations. Differences in egg parasitism between shaded and open plantation areas

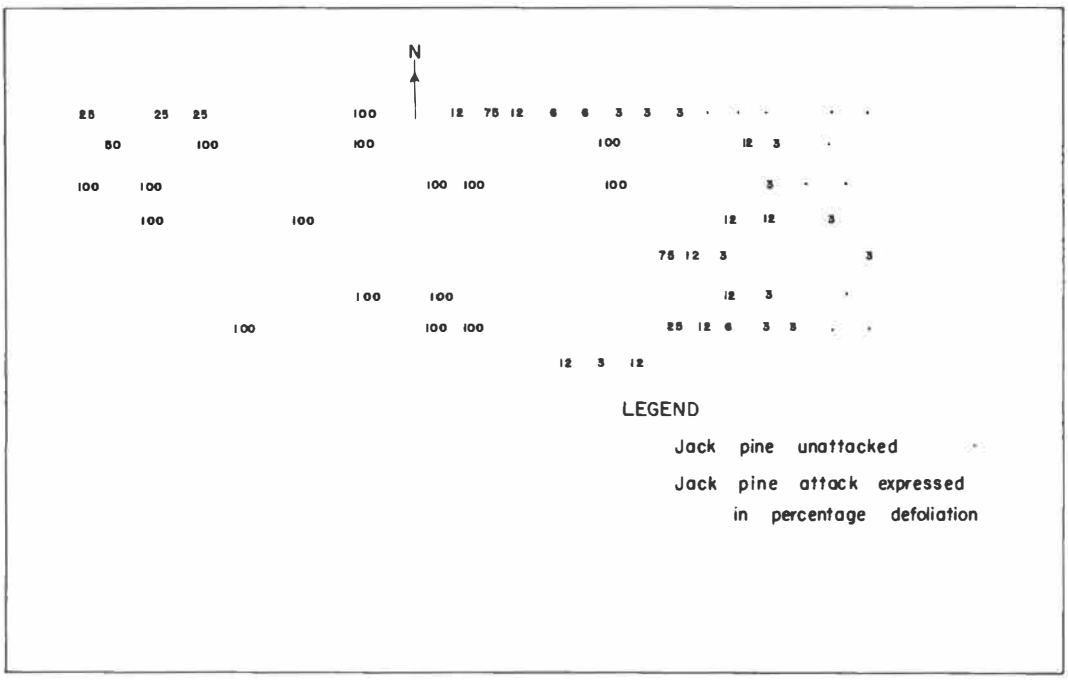


FIGURE 44. DIAGRAM OF JACK PINE PLANTATION ILLUSTRATING HEAVY RED-HEADED PINE SAWFLY ATTACK IN AREA OF POOR SURVIVAL.

could not account for the continued differential attack in the shaded areas. During the egg parasite survey of 1947 and 1948 both open-growing and shaded pines were carefully examined. Eggs were found only in the shaded portions of the plantations. Figure 45 illustrates the reservoir areas within a shortleaf pine plantation. The gray patches are sassafras and persimmon overtopping the pines which were heavily attacked by the sawfly during the endemic period. Figure 46 illustrates a border patch of hardwoods shading another reservoir area of shortleaf pine. Reservoir populations were maintained in these areas during 1948 and during the first generation in 1949. Defoliation in these shaded areas increased during the second generation in 1949, while in the third generation sawfly activity increased markedly on the forest as a whole. As was expected, heavy infestations were encountered in the shaded areas and only scattered defoliation in the open areas.

(Open Plantations)

Reservoir sawfly populations were also observed to be maintaining themselves on the open wide-spaced pines in localized areas (Figure 26). Scattered defoliation of such trees was observed on many plantations throughout the forest during 1948 and 1949. Heavy defoliation was encountered during third generation activity in 1949.

Manistee National Forest

During the endemic period in 1949, plantation sites tentatively considered as representing sawfly reservoir areas were examined for the red-headed pine sawfly. Low populations of sawflies were observed on all of the susceptible areas. In the shaded plantations on the Manistee Ranger District, low populations continued to defoliate the shaded survivors of the 1946-1948 outbreak. Examinations of several plantations on the Cadillac Ranger District indicated that the reservoir populations were maintaining themselves on the plantation edges, under hardwood shade and in the sandblow sites. Open plantations and plantations where the crowns had closed appeared practically free of sawfly activity. Re-examination of the central hardwood and the edge-hardwood sites discussed previously indicated that volunteer reproduction developing in the vicinity of the sawfly killed pines was again being attacked. These volunteers on the central hardwood plots and on the border-hardwood plots were closely examined for sawfly activity. The location of each seedling and the presence or absence of sawflies on one of these study areas is shown diagrammatically in Figure 47. The seedlings attacked and the attacked living trees of the original plantation are indicated. On this plot seven of the 34 volunteer seedlings and six of the trees originally planted were attacked in 1949. Fourteen egg batches were counted on the seedlings and 14 on the original trees. One of ten volunteer seedlings observed in the shaded area between the two east border hardwoods in Figure 30 was infested in 1949.

Other National Forests Visited

Currently severe sawfly outbreaks on the Chequamegon National Forest are causing heavy defoliation on the red and jack pine plantations

FIGURE 45. RED-HEADED PINE SAWFLY POPULATION RESERVOIR AREAS IN SHADED PORTIONS OF SHORTLEAF PINE PLANTATION. GREY AREAS ARE PERSIMMON AND SASSAFRAS CLUMPS SHADING PINES.

FIGURE 46. RED-HEADED PINE SAWFLY POPULATION RESERVOIR AREAS UNDER BORDERING HARDWOODS.

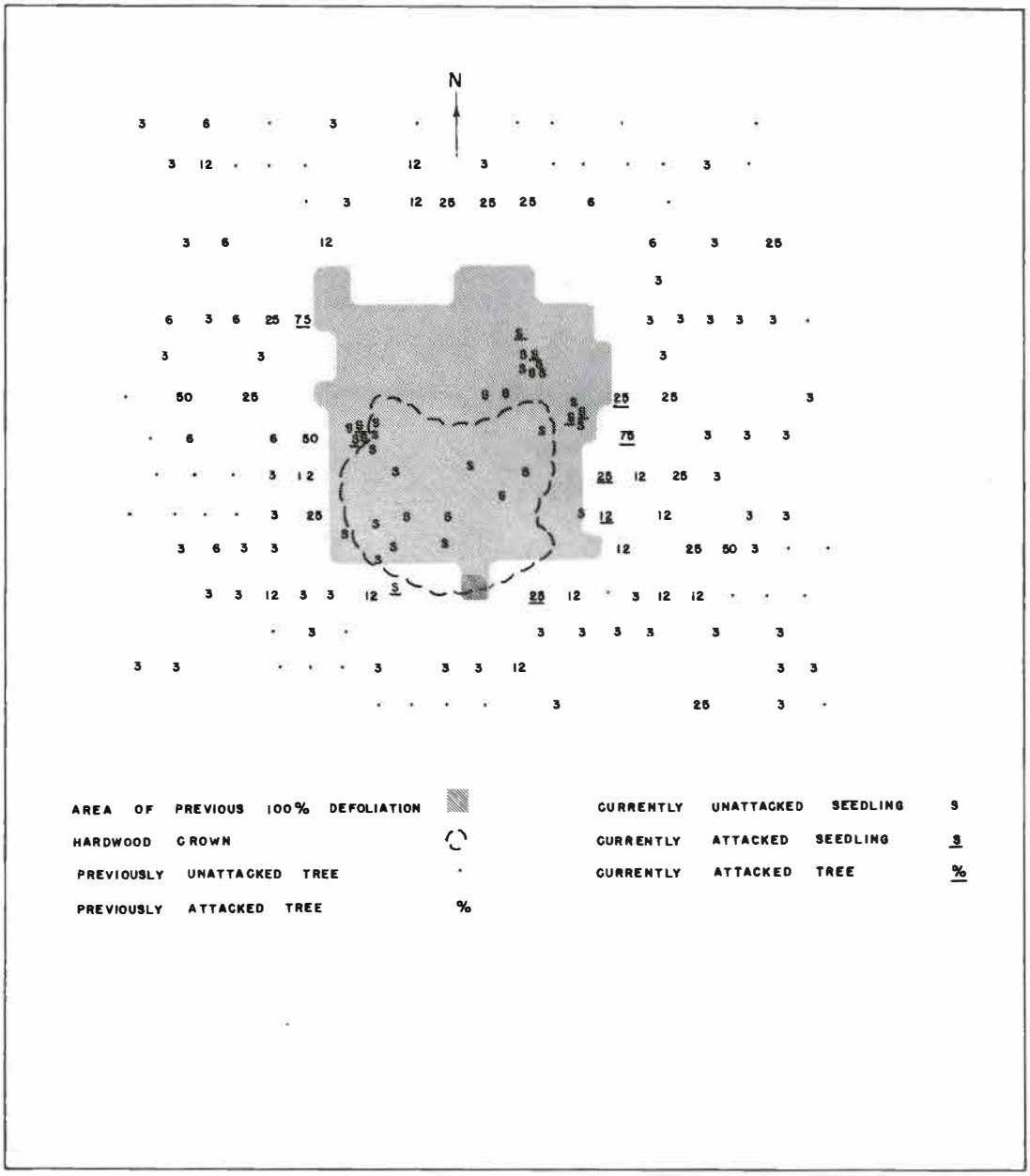


FIGURE 47. DIAGRAM OF JACK PINE PLANTATION ILLUSTRATING HEAVY RED-HEADED PINE SAWFLY ATTACK OF VOLUNTEER REPRODUCTION IN VICINITY OF HARDWOOD CROWN.

growing under aspen overstories. On the Mark Twain National Forest in southwest Missouri, a small population seems to be maintaining itself in the shortleaf plantings under oak. Reservoir populations were observed on the Nicolet National Forest in north central Wisconsin.

In general, little information concerning sawfly population reservoirs on other national forest areas within this region is available. Complaints of sawfly damage are voiced only after outbreak or near outbreak populations cause economic losses. Observers reporting sawfly outbreaks usually consider the plantations as a whole, omitting any reference to the suppressed and poor vigor trees which were defoliated and killed. Death of these trees could be misinterpreted as due to intolerance or competition casualties.

Summarily speaking, site selected by ovipositing female red-headed pine sawflies appeared to be largely governed by light or by some light-related phenomenon. Associated with shaded sites - or the absence of light - may be lower temperature, higher relative humidity (greater saturation deficit), reduced air movement, or a combination of these factors. In addition, a variation in needle characteristics may exist due to action of these foregoing factors. Variation in cuticle hardness or thickness, mesophyll depth, variations in needle serrulations and unknown or imponderable characteristics may also have influenced site selection. The modus operandi of the shade preference was not determined.

Host-Site Susceptibility

Throughout the red-headed pine sawfly investigations it has become increasingly evident that certain pine species and, within a particular species, certain definite sites were preferred or selected for attack. Host preference data assembled for the United States and Canada were discussed above. To supplement this, the writer has attempted to assemble a listing of site-host conditions most susceptible to sawfly attack on the Shawnee and Manistee National Forests. In the following site-host susceptibility listing are only those situations or sites observed to be attacked by the red-headed pine sawfly. Such sites as shaded Virginia and jack pine on the Shawnee were omitted because no instance of these were observed. In the sequence of susceptibility, the most susceptible species and site are listed first. Successful silvicultural control of the sawfly lies in the avoidance of the situations high in the following listing:

Shawnee National Forest	Manistee National Forest
Shaded shortleaf pine	Shaded jack pine
Scattered shortleaf pine	Sandblow jack pine
Edge shortleaf pine	Edge jack pine
Isolated shortleaf pine	Isolated jack pine
Shaded pitch pine	Shaded red pine
Open-growing shortleaf pine	Sandblow red pine
Open-growing pitch pine	Edge red pine
Open-growing loblolly pine	Open-growing jack pine
Open-growing Virginia pine	Isolated red pine
Open-growing jack pine	Open-growing red pine

Shawnee National Forest (continued)

Closed shortleaf pine
Closed pitch pine
(Edge-growing red pine
(Open-growing red pine
(Closed-growing red pine

Manistee National Forest (continued)

Closed jack pine
Closed red pine

Meteorological Influences

The profound influence exerted by climatic factors (temperature, moisture, light, and atmospheric components) on animal and plant populations is well recognized. Detailed studies and casual observations, too numerous to mention here, have been made on the effects of one or a combination of the foregoing factors on insect survival, distribution, and development.

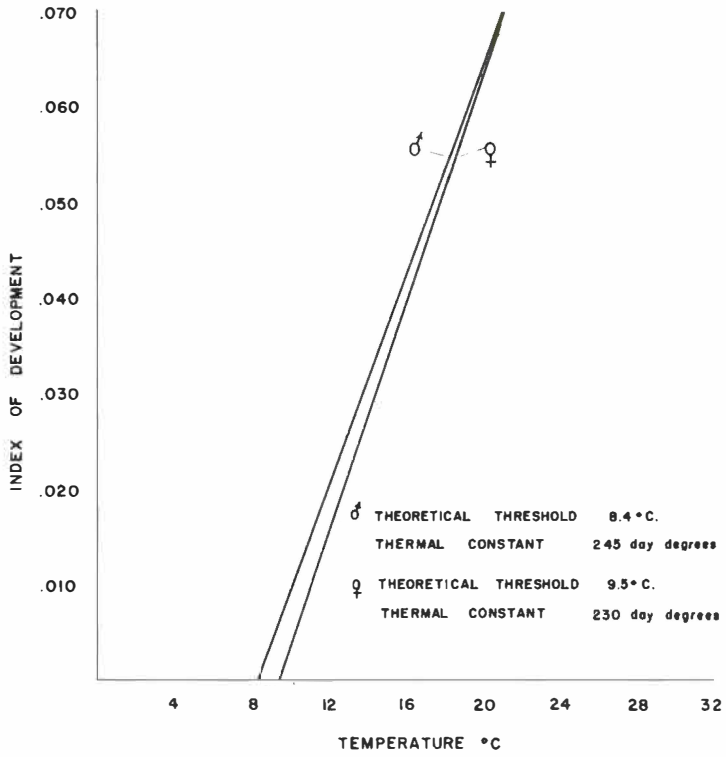
Studies of the influences of climatic factors on the red-headed pine sawfly are few. With the exception of three papers, a small section of Middleton's (1921) publication, Brown and Daviault's (1942) paper on the influence of temperature on the development after hibernation in the cocoon, and the section of Daviault's (1949) unpublished manuscript on the effect of temperature on the emergence of the red-headed pine sawfly adults, casual observations form the information available for this species.

Temperature

The early emergence of adult red-headed pine sawflies from cocoons spun in sites exposed to maximum amounts of daily heat has been observed by numerous field workers. Also, the early appearance of sawfly adults following abnormally mild springs has been commented upon. Daviault (1949) reported that the peak of abundance of adult emergence generally coincided with similar peaks on air temperature curves and that emergence was more rapid from cages well exposed to direct sunlight. A decrease in the percentage of sawflies emerging and an increase in the time of emergence was encountered as depth of cocooning increased. Daily emergence records revealed that female and male emergence began in the morning as soon as the heat of day was felt, and practically all adults emerged between 8:00 a.m. and noon.

Brown and Daviault (1942) compared the influence of temperature on the development of several sawflies after hibernation in the cocoon and computed the time temperature constants and theoretical thresholds of development. They found that *N. lecontei* had the highest theoretical threshold of development of the 8 species of sawflies investigated in Canada. The red-headed pine sawfly females had a theoretical threshold of 9.5° C. and the male sawflies 8.4° C. with thermal constants of 230 day degrees respectively, Graph 8. Under field conditions, a 2.6 percent decrease in time was encountered as compared to laboratory reared females and 2.0 percent reduction for field reared males.

Little information concerning the influence of temperature on adult sawfly activity is available in the literature. The writer observed



GRAPH 8. RATE OF DEVELOPMENT OF RED-HEADED PINE SAWFLY AFTER HIBERNATION IN THE COCOON (BROWN AND DAVIAULT, 1942).

red-headed pine sawflies ovipositing at air temperatures as high as 108° F. and as low as 46° F. Oviposition time - the time consumed in cutting the egg pocket in the needle, laying the egg, and moving to the next egg pocket site - varied according to temperature. At 90° F., oviposition averaged 49 seconds per egg, while at 52° F. oviposition time averaged 143 seconds. Between 60° F. and 70° F., oviposition time averaged 1-1/2 minutes per egg.

Egg incubation time appeared to be closely associated with atmospheric temperature. Egg hatching occurred earlier during periods of high temperatures and was markedly delayed during periods of low temperatures. Middleton (1921) reported egg incubation times of 21, 16, and 13 days at mean temperatures of 71.23° F., 74.59° F., and 78.8° F. respectively at Falls Church, Virginia. Mavisalt (1949) reported mean incubation periods of 25 days at 64° F. and 20 days at 67° F. in Quebec, Canada. On the Shawnee National Forest, egg incubation periods averaged 20, 15, and 24 days during the first, second, and third generation activity periods in June, August, and September, respectively. Sawfly eggs laid on the Shawnee during late November, 1947, did not hatch during the fall, nor did they hatch after over-wintering.

Information concerning the influence of temperature on larval activity is also meager. Middleton (1921) observed that larval feeding was reduced during cool cloudy days and accelerated during warm days. The writer has observed a reduction in the feeding intensity when temperatures neared 100° F. and a complete cessation below 55° F.

The severe mortality among migrating sawfly larvae caused by high sand temperatures on the Manistee National Forest in 1949 was discussed in a foregoing section. Larval survival was less than 3 minutes when sand temperatures above 105° F. were encountered and many larvae succumbed during migrations, as illustrated in Figure 48. Sawfly larvae survived temperatures as low as 22° F. on several occasions during 1947 on the Shawnee National Forest, and resumed their feeding during the warmer portions of the day when the air temperatures again rose.

Moisture

Information concerning the influence of moisture on red-headed pine sawfly activity is scant. Middleton (1921) surmised that egg hatch was closely associated with relative humidity. He cited that at an average of 74 percent relative humidity the eggs hatched in 21 days, and at 68 percent relative humidity hatch was reduced to 18 days. At 65 percent relative humidity hatching occurred after 13 days. He added, however, that normal hatch was probably greatly influenced by a balance of the light and moisture with limits and optima existing. Brown and Mavisalt (1952) observed that red-headed pine sawfly survival in the cocoon stage was greater at 40 to 45 percent relative humidity than at 90 to 95 percent relative humidity. Also, the threshold of development was lower in the more moist atmospheres. Female sawfly threshold of development was 10.0° C. in the 90 to 95 percent relative humidity range as compared to 9.5° C. in the 40 to 45 percent relative humidity range. Male threshold temperatures were 9.4° C. and 8.4° C. respectively.

FIGURE 48. HEAVY RED-HEADED PINE SAWFLY LARVAL MORTALITY DURING MIGRATIONS FROM DEFOLIATED JACK PINE. DEATH WAS DUE TO HIGH SURFACE TEMPERATURES.

Light

In view of the apparent shade-infestation relationship exhibited by the red-headed pine sawfly throughout the study areas, it was deemed advisable to investigate more closely the shadow patterns cast by the border and central hardwoods in areas of severe sawfly injury. The lateness of initiating field studies on the Manistee National Forest in 1948 and 1949 prevented shadow pattern measurements during the sawfly oviposition period. Shadow pattern measurements were begun, however, in mid-June 1949 and continued into August. Measurements were taken every 7 to 10 days, whenever cloud cover did not interfere, along the four cardinal directions and along intermediate directions. Measurements were made at two-hour intervals throughout the day.

Red-headed pine sawfly emergence on the Manistee National Forest has reached its peak during the first week of June for the past four years according to local observations by Forest Service personnel. Oviposition generally begins soon after emergence and also reaches its peak during this period. For this reason, it was believed that the shadow patterns cast by the hardwood crowns during the first week of June should closely coincide with the areas of severe infestation in the vicinity of the hardwoods if a shade-infestation relationship existed. In the absence of an "oviposition week" shadow pattern, the shadow pattern cast during the week of July 10th, 19 days after the longest day of the year was selected as that most similar to the shadow pattern cast during the first week of June, approximately 19 days prior to the longest day. Only the 10:00 a.m., 12:00 m., and 2:00 p.m. shadow patterns were considered because the 8:00 a.m. and 4:00 p.m. shadows were practically horizontal. Figures 49 and 50 illustrate the close agreement between the shadow patterns cast at 10:00 a.m., 12:00 m., and 2:00 p.m. and the severe infestation and defoliation in the vicinity of these hardwoods. The Hill and areas of heavy infestation coincided with the shadow patterns which extended to the north side of the hardwoods.

While the shaded pines appeared to be selected for oviposition when a choice was presented, and the densest needle clusters were selected on the open-growing pines, the absence of light alone should not be designated as the sole factor influencing egg site selection. Other physical factors commonly associated with decreased sunlight may also have influenced egg site selection. Differences in needle characteristics which conceivably influence site selection may occur under these varied conditions. At present, it would seem that light was one of the prime factors acting in the site acceptability sequence; final needle selection or rejection was probably based primarily on needle characteristics.

Predicted Number of Generations Per Year

The close relationship between the length of the growing season and the number of generations per year of several of our multi-generation crop pests has been observed by numerous entomologists. Much research has been conducted to determine the estimated number of generations per year of such pests as the European corn borer, Pyrausta nubilalis (Hbn.), the Mexican bean beetle, Epilachna varivestris Muls., and the codling moth, Carpocapsa pomonella (L.).

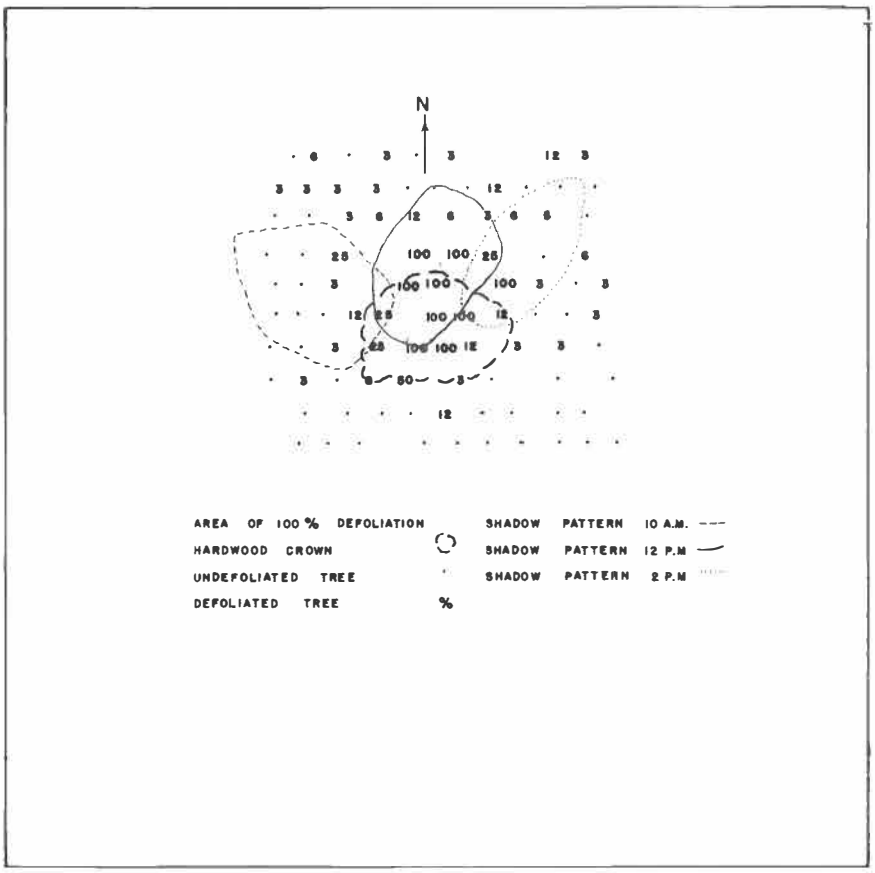


FIGURE 49. DIAGRAM OF JACK PINE PLANTATION ILLUSTRATING RELATIONSHIP BETWEEN HARDWOOD SHADOW CAST DURING RED-HEADED PINE SAWFLY OVIPOSITION PERIOD AND HEAVY SAWFLY ATTACK.

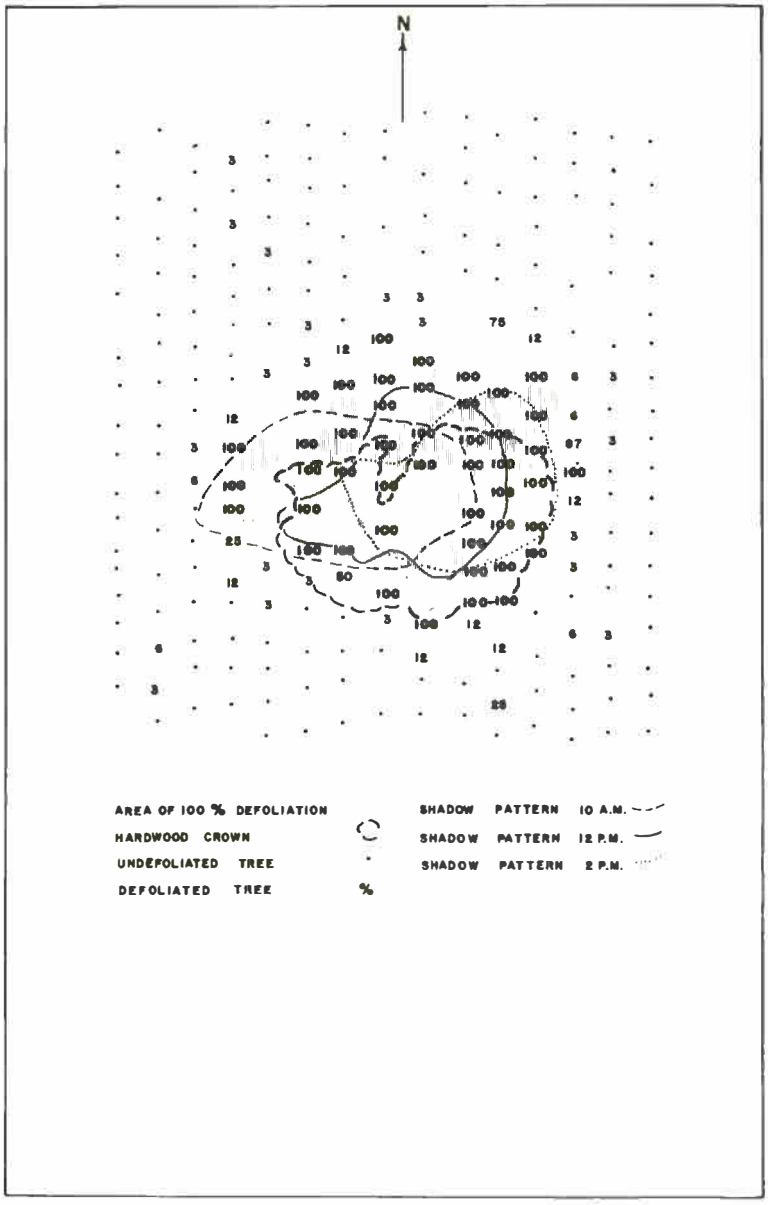


FIGURE 50. DIAGRAM OF JACK PINE PLANTATION ILLUSTRATING RELATIONSHIP BETWEEN HARDWOOD SHADOW CAST DURING RED-HEADED PINE SAWFLY OVIPOSITION PERIOD AND HEAVY SAWFLY ATTACK.

Although the information concerning the number of generations per year of the red-headed pine sawfly is meager, an attempt was made to assemble life history data as a basis for predicting the number of generations per year for this sawfly. Map 3 shows the average length of growing season (frost free days) for Eastern United States, based on records for 39 years, Kincer (1941). Superimposed on these data are the available records of the number of generations per year of the sawfly. On the basis of this limited information the number of generations per year for the various growth zones can be predicted as follows:

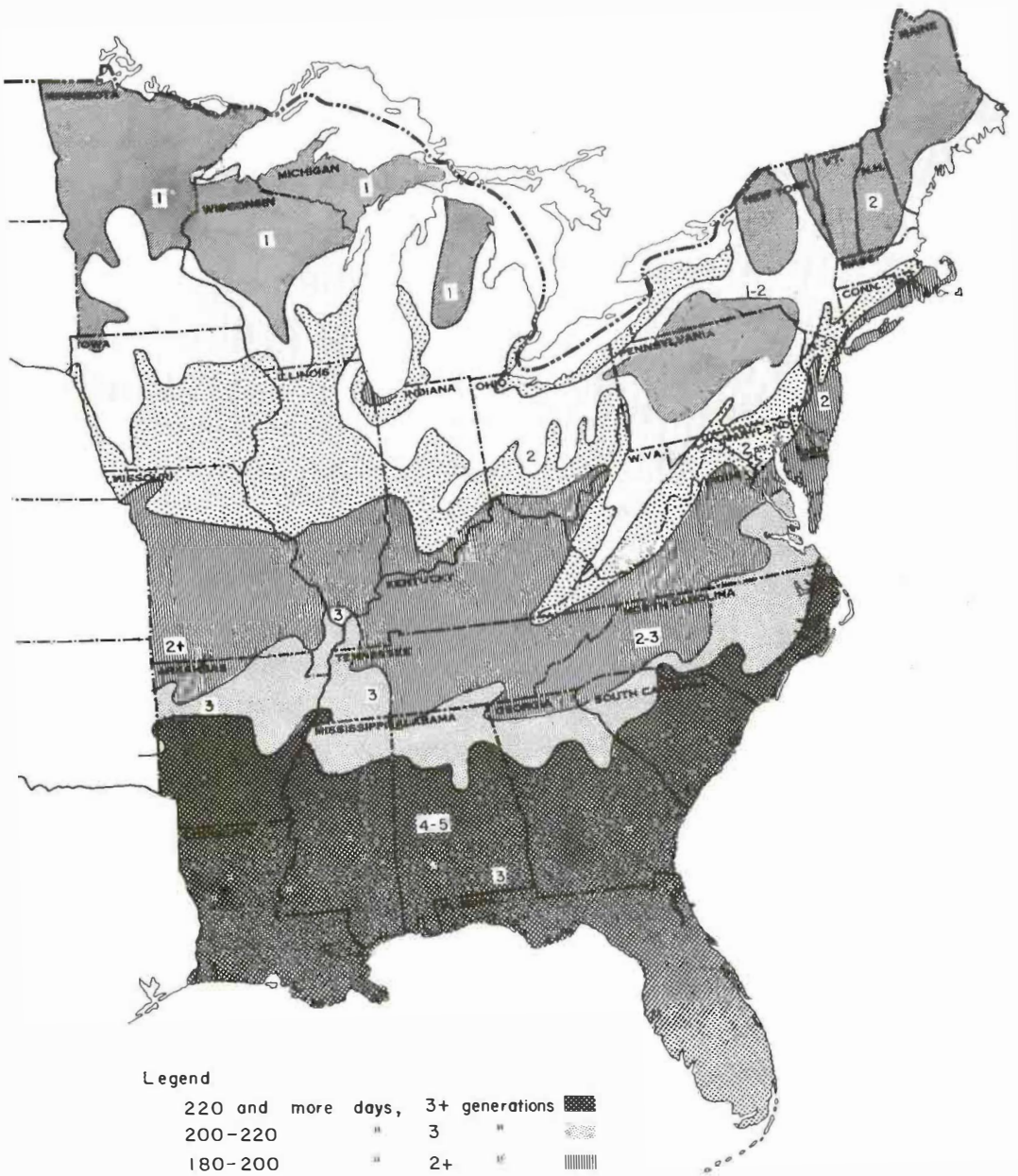
Above 220 days	3 -
200 - 220 "	3
180 - 200 "	2 -
160 - 180 "	2
140 - 160 "	1 -
Below - 140 "	1

Since the foregoing predictions are based on average growing seasons, some deviation could be expected during exceptionally long or short growing seasons. In the southern reaches of the sawfly range 4 - 5 generations are occasionally reported while in the North, the single generation may be active well into October during a late season.

Host Survival

The effects of partial and complete defoliation of coniferous trees have been investigated by numerous individuals. Among the most important works may be mentioned Harper (1913), Craighead (1927, 1940), Graham (1931), Baker (1941), and Beal (1942). For the most part, complete defoliation killed the majority of the conifers. Deformity and growth reduction resulted from partial defoliation insufficient to cause the death of these trees. Among the hard pines attacked by the red-headed pine sawfly, only a few of the southern pines have been reported able to survive complete defoliation. In the northern part of the United States and in Canada, jack and red pines succumb to a single complete defoliation. Complete defoliation of single branches normally resulted in the death of that part of the tree. Incompletely defoliated branches may, however, survive if a few needles or partially consumed needles remain. In the southern part of the United States shortleaf, loblolly, slash, and longleaf pines have been reported able to survive complete defoliation. Beal (1942) reported that open-growing shortleaf and loblolly were able to better withstand red-headed pine sawfly defoliation than pines growing in competition with over-topping hardwoods. He found mortality of unshaded trees resulting from single late summer defoliation only when more than 75 percent of the foliage had been destroyed. Eighty-four and two-tenths percent mortality occurred among open-growing pines from which 76 to 100 percent of their foliage was removed. One-third of the shaded pines died when 26 to 50 percent of the foliage was removed. Fifty-five percent of the shaded pines in the 50 to 75 percent defoliation class died, and 96.5 percent of the 75 to 100 percent defoliation class died. Lack of light, severe root competition, and larval bark feeding were mentioned as possible additional factors influencing survival.

MAP 3. PREDICTED NUMBER OF GENERATIONS PER YEAR OF THE RED-HEADED PINE SAWFLY BASED ON LENGTH OF GROWING SEASON.



Legend

220 and more	days,	3+	generations
200-220	"	3	"
180-200	"	2+	"
160-180	"	2	"
140-160	"	1+	"
140 and less	"	1	"

Reported generations per year

During 1947 the writer tagged 125 open-growing shortleaf pine trees defoliated in varying degrees on the Shawnee National Forest for survival studies. The prime objective of this study was to ascertain whether these pines could survive complete or partial defoliation, and, also, to determine subsequent recovery. Tree heights were measured to the nearest foot. The percent defoliation was estimated, and survival and vigor observations were made periodically. In November 1949, all tree heights were re-measured and several trees were cut for radial growth measurements. While the initial objective was to determine survival at various defoliation levels, certain additional general trends were obtained from these studies. Defoliation injury to the shortleaf pine will be discussed from the viewpoint of vigor and mortality, height growth reduction, and general trends in radial growth reductions.

Mortality and Height Growth

(Third generation defoliation - 1946)

Two plots of 22 shortleaf pines each planted in 1942 and known to be completely defoliated during third generation sawfly activity in 1946, and possibly also during second or first generation activities in 1946, were tagged for recovery studies on June 6, 1947. A small square of phloem was removed from the base of each tree with a knife, the height of the tree measured, and the presence or absence of sprouts noted. Current Nantucket pine moth (Rhyacionia frustrana (Comst.)) injury was observed on all trees on the two plots. No defoliation occurred on these plots during 1947, 1948, or 1949 subsequent to the 100 percent 1946 defoliation. Nantucket pine moth populations continued high on all forest plantations during 1947 and 1948.

On one plot all 22 trees sprouted throughout their entire length during early 1947 (Figure 51). Examinations of this plot in November 1949 indicated that all trees had survived the defoliation and were growing vigorously. The average height of the trees on June 6, 1947 was 3.6 ± 0.26 feet. On November 8, 1949, the average height was 8.6 ± 0.35 feet, indicating an average height growth of 5.0 ± 0.21 feet during the 3-year period. On the second plot one tree was dead in June 1947, and two additional trees died during the following 3-year period. The average height of the 19 trees which survived the complete 1946 defoliation, was 3.2 ± 0.19 feet on June 6, 1947 and 6.7 ± 0.38 feet on November 8, 1949. An average of 3.5 - 0.20 feet of height growth was put on between the foregoing two dates. Figure 52 illustrates the present vigor of these shortleaf pine trees in November 1949.

(First Generation Defoliation - 1947)

Plots were established for recovery studies in 3 plantations heavily defoliated during first generation sawfly activity in 1947. Twenty shortleaf pines in an open 1941 plantation, which sustained varying degrees of sawfly defoliation, were tagged and measured on July 16, 1947. All twenty trees were growing vigorously on November 4, 1949 when height measurements were made. Height growth for the five defoliation classes and one check class were as follows:

FIGURE 51. SHORTLEAF PINE RECOVERY IN SPRING OF 1947 FOLLOWING COMPLETE THIRD GENERATION 1946 DEFOLIATION BY RED-HEADED PINE SAWFLY.

FIGURE 52. SHORTLEAF PINE RECOVERY BY FALL OF 1949 FOLLOWING COMPLETE THIRD GENERATION RED-HEADED PINE SAWFLY DEFOLIATION IN 1946.

Percent Defoliation	Average Height Growth (Feet)	Number of Trees
100	5.0	5
96	4.0	3
75	5.0	2
50	5.5	2
25	5.0	5
CK	5.0	3

The severity of first generation defoliation was not reflected in the height growth put on during the 3-year study period. The influence of defoliation on height growth was probably masked by the heavy Nantucket pine moth infestation which was practically 100 percent during 1947 and 1948.

Ten open-growing shortleaf pines planted in 1942 were tagged and measured on July 16, 1947. All trees were growing vigorously on November 5, 1949. Again no height growth difference could be demonstrated in the following tabulation:

Percent Defoliation	Average Height Growth (Feet)	Number of Trees (Basis)
96	3.0	1
50	3.6	3
25	3.0	1
CK	2.5	2

Thirty open-growing shortleaf pines planted in 1941 were tagged and measured on three plots on July 17, 1947. All trees survived and were vigorously growing on November 6, 1949 (Figures 53 and 54) when the heights were again measured. Height growth differences were as follows:

Percent Defoliation	Average Height Growth (Feet)	Number of Trees (Basis)
100	4.5	11
96	4.5	2
87	3.0	1
75	5.6	3
50	6.0	5
25	5.5	2

The differences barely appear to reflect defoliation intensity among the 24 trees measured in 1949. One hundred percent and 96 percent defoliated trees appeared to show slightly less height growth than the 75 percent and lower defoliation classes. With these few data significance is questionable.

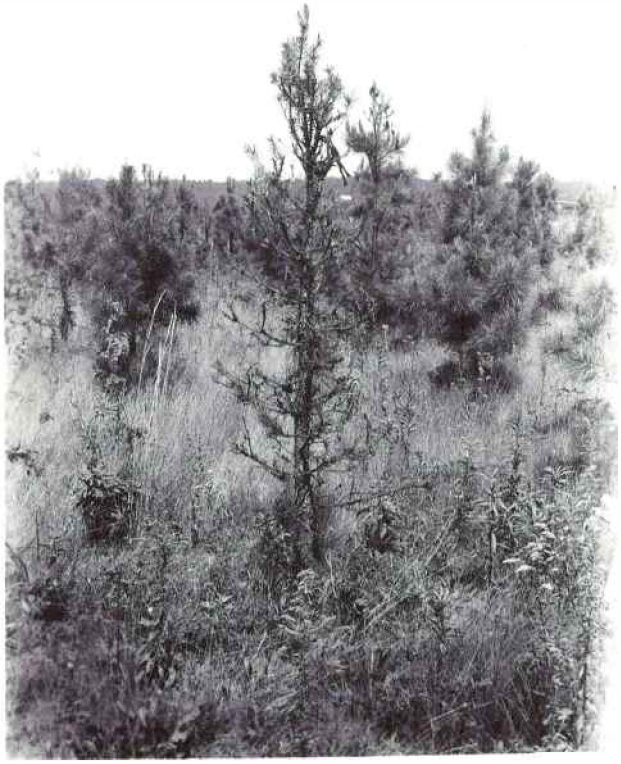


FIGURE 53. SHORTLEAF PINE TREE 134 FOLLOWING COMPLETE FIRST GENERATION RED-HEADED PINE SAWFLY DEFOLIATION IN 1947. UPPER BRANCHES AND LEADER HAD BEGUN TO REFOLIATE PRIOR TO COMPLETION OF LARVAL FEEDING.

FIGURE 54. SHORTLEAF PINE TREE 134 FULLY RECOVERED AT END OF 1949 GROWING SEASON.

(Second Generation Defoliation - 1947)

Twenty trees were tagged on September 5, 1947 and measured following a single complete second generation sawfly defoliation. All pine trees recovered and were growing vigorously on November 6, 1949 when they were re-measured. The average height growth of these trees was 3.3 ± .21 feet.

(Summary)

Shortleaf pine mortality on the Shawnee National Forest plots due to red-headed pine sawfly defoliation was negligible. Only 3 of 44 tagged shortleaf pines completely defoliated during third generation activity in 1946 died as a result of the attack. Forest Service personnel estimated less than 10 percent mortality in an open (Bay City) shortleaf planting defoliated in 1945 and possibly three times in 1946.

Height growth expression of the defoliation was lacking probably because of heavy leader destruction through Nantucket pine moth attack. Despite this damage during 1947 and 1948, height growth averaged 4.3 feet on the trees 100 percent defoliated by third generation larvae in 1946, approximately 3.0 feet to 5.0 feet on trees defoliated by first generation larvae in 1947, and 3.3 feet on trees defoliated by the second generation larvae in 1947.

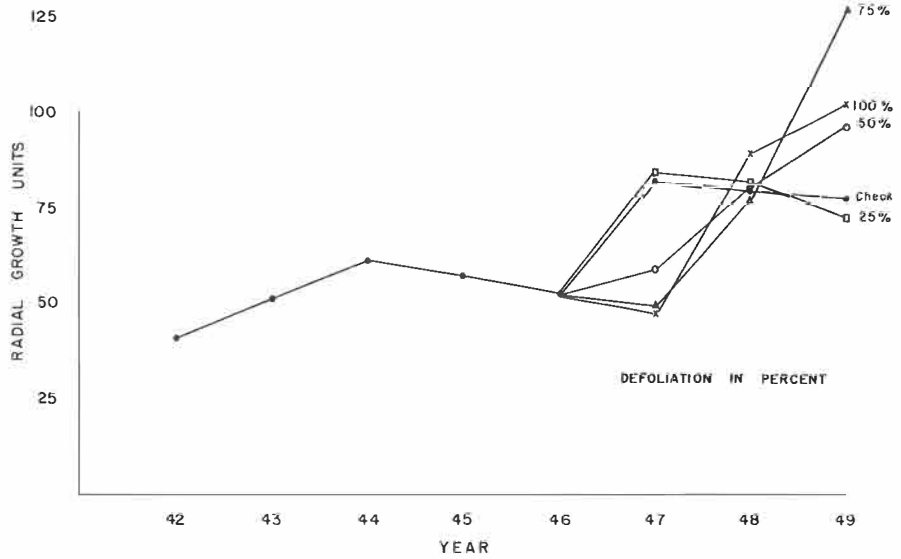
Radial Growth

A number of shortleaf pine trees from the defoliation classes on the study plots discussed in the preceding section were cut 6 inches above the ground in November 1949 for radial growth determinations. Wafers or discs were removed and annual radial growth determined by averaging measurements on 4 cut radial surfaces. Radial growth of the first ring, i. e. the ring next to the pith, was ignored in computing growth. In most instances this allowed growth determinations for the year following planting through 1949. Radial growth appeared to reflect in general the influence of partial and severe sawfly defoliation much better than did height growth.

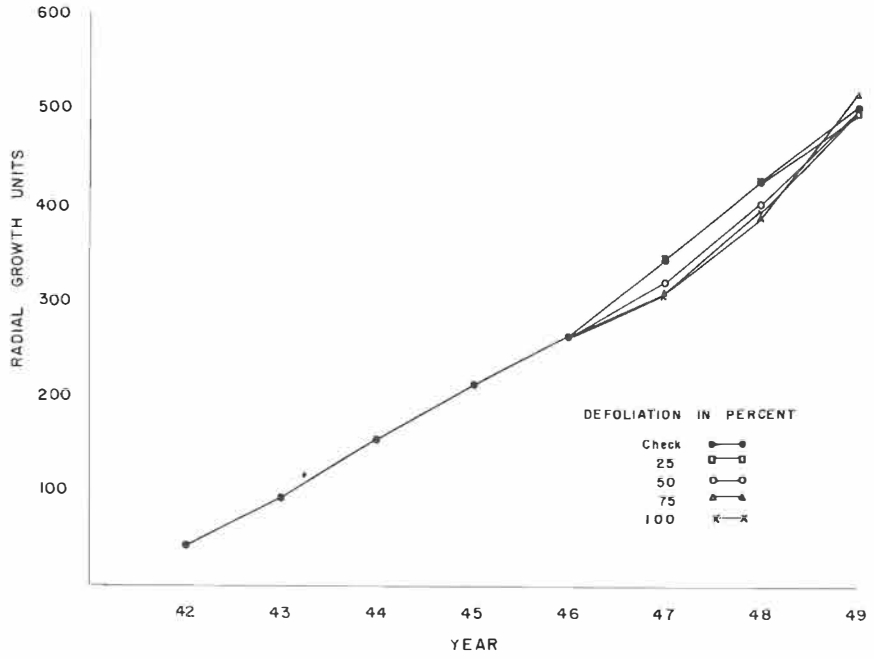
(First Generation Defoliation)

The influence of heavy first generation 1947 sawfly defoliation on annual radial growth on a 1941 shortleaf pine plantation, is indicated on Graph 9. Average annual radial increment of the non-defoliated 25, 50, 75, and 100 percent defoliation classes was plotted as a single average to illustrate the behavior of these trees through 1946. Average radial growth for the 2 trees per defoliation classes and the 2 check trees was plotted separately for each class subsequent to 1946 to illustrate the effects of varying degrees of defoliation.

The average accumulative radial growth per year for all trees through 1946 and for the non-defoliated and defoliated classes in 1947, 1948, and 1949 are plotted on Graph 10. Average accumulated radial growth of the check and 25 percent defoliated trees followed the same pattern of a gradual increase in growth rate in 1947, and a slight decrease in 1948 and 1949. The 50, 75, and 100 percent defoliation



GRAPH 9. EFFECT OF FIRST GENERATION RED-HEADED PINE SAWFLY DEFOLIATION ON ANNUAL SHORTLEAF PINE INCREMENT.



GRAPH 10. EFFECT ON FIRST GENERATION RED-HEADED PINE SAWFLY DEFOLIATION ON ACCUMULATIVE ANNUAL SHORTLEAF PINE INCREMENT.

classes showed decreases in 1947 radial increment in this same relative position and corresponding increase in 1948 and 1949. Figure 55 illustrates the annual ring growth picture of one non-defoliated tree. Figure 56 illustrates the reduced annual growth ring caused by complete first generation 1947 defoliation and the subsequent recovery in 1948 and 1949.

The information obtained on this plot indicates that the radial increment was temporarily but not permanently reduced in the 50, 75, and 100 percent defoliation classes during the year the damage occurred. However, recovery was rapid and two years later the trees appeared to have increased their annual growth rate and to have made up the increment lost during the years of injury.

The general effects of first generation 1947 sawfly defoliation on radial growth on a 1941 plantation followed the same trend in growth reduction pattern exhibited on the foregoing area. Graph 11 illustrates the average radial growth pattern for all trees through 1946, the increasingly greater radial growth reduction in 1947 as the severity of the defoliation increased, and the remarkable 1948 and 1949 recoveries. On Graph 12, a charting of the average accumulative growth, the 2 trees, each in the 50 and 75 percent defoliation classes, appeared to have regained their growth rate previous to 1947. The trees in the 100 percent defoliation class apparently recovered more slowly. No non-defoliated trees were available in the plantation area.

(Second Generation Defoliation)

The average annual radial increment of four trees 100 percent defoliated in 1947, was determined and plotted on Graph 13. The average annual radial increment of two first generation 1947 100 percent defoliated trees was also indicated for comparison purposes.

First generation defoliation in 1947 caused an immediate decrease followed by a rapid recovery in 1948 and a slight growth decline in 1949. No marked decline in the radial increment was apparent in 1947 by the trees completely defoliated during second generation. The influence of the second generation was reflected in a decrease in growth the following year, and an increase in 1949. Complete first generation defoliation resulted in a decline in the accumulated growth rate in 1947 and an increase in 1948 (Graph 14). Complete second generation defoliation apparently came after the major portion of the yearly increment had been attained, and hence no rate decline was observed. The decline in this group was delayed until the 1948 season and was followed by a marked 1949 increase. Examination of these two average accumulative radial increment curves suggests that these defoliated trees have regained their increment losses within two years of defoliation. Figure 57 illustrates the 1948 annual ring reduction resulting from complete second generation 1947 sawfly defoliation.

(Third Generation Defoliation)

Two plots of 22 trees each were selected for survival and growth recovery studies in a shortleaf pine plantation which had suf-

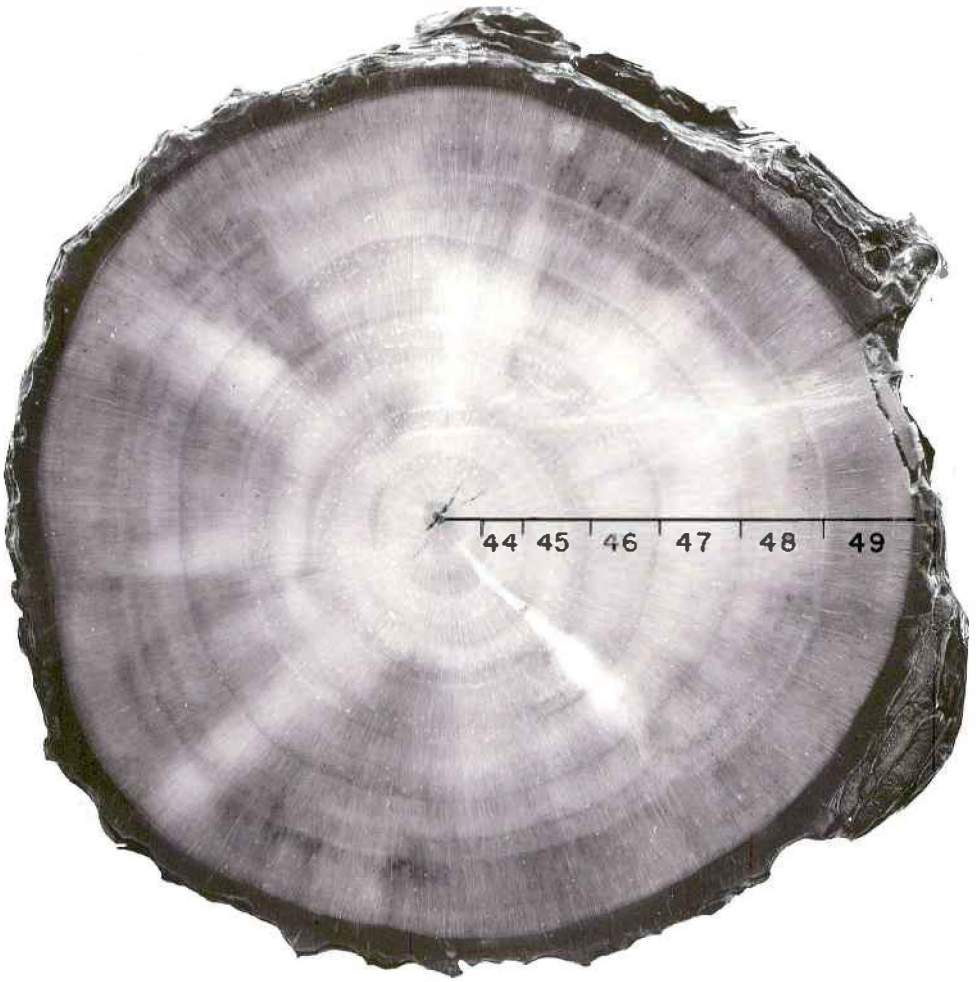
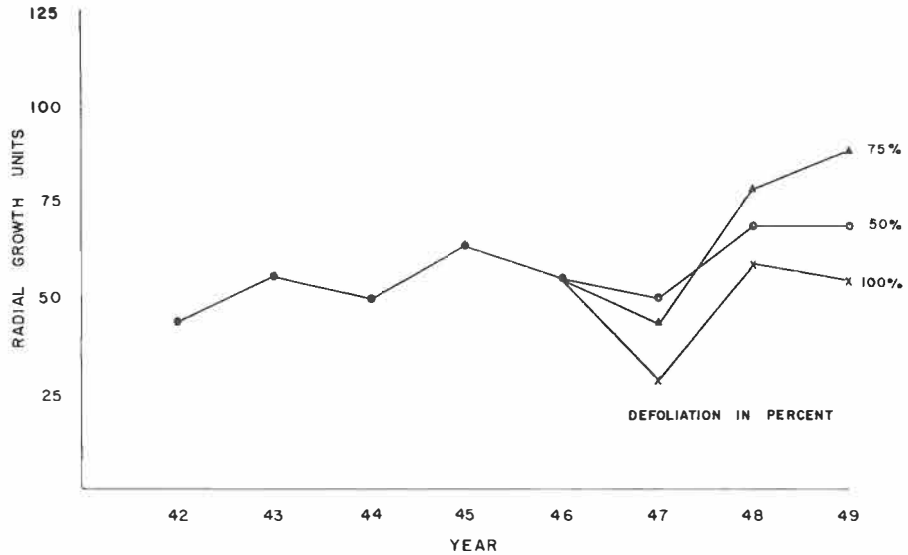
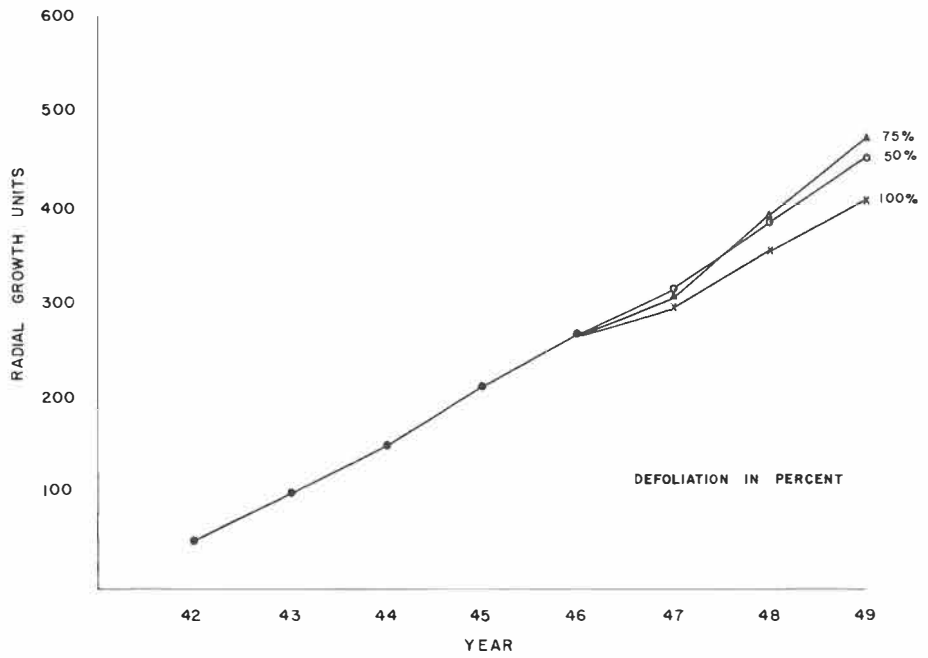


FIGURE 55. SHORTLEAF PINE ILLUSTRATING NORMAL ANNUAL RING GROWTH.

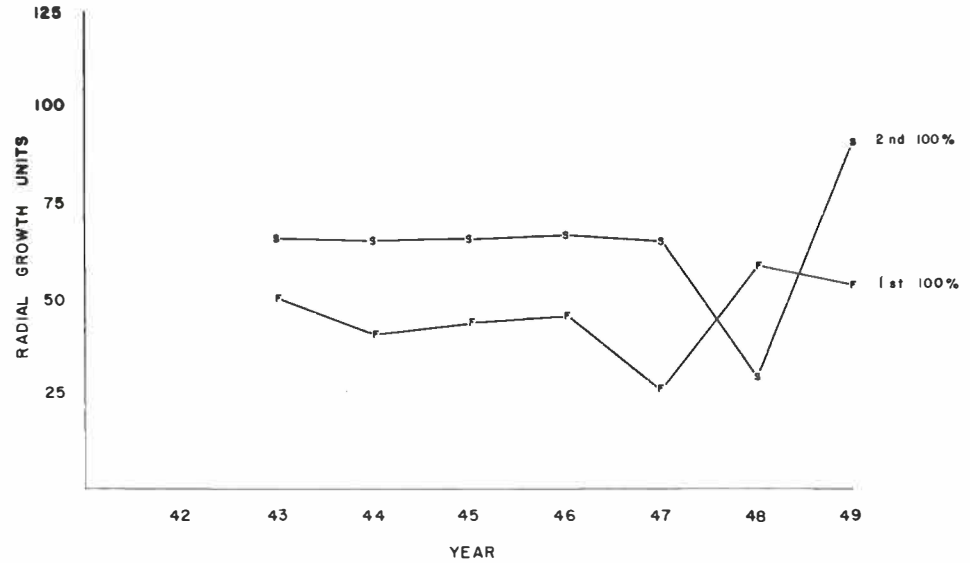
FIGURE 56. SHORTLEAF PINE ILLUSTRATING REDUCED 1947 ANNUAL RING CAUSED BY COMPLETE FIRST GENERATION RED-HEADED PINE SAWFLY DEFOLIATION.



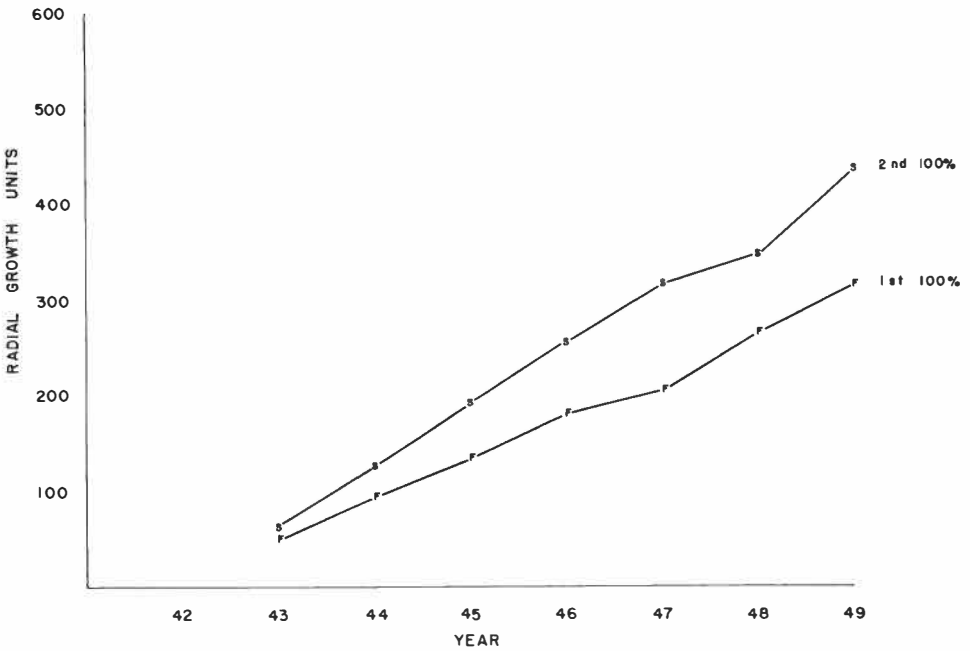
GRAPH 11. EFFECT OF FIRST GENERATION RED-HEADED PINE SAWFLY DEFOLIATION ON ANNUAL SHORTLEAF PINE INCREMENT.



GRAPH 12. EFFECT OF FIRST GENERATION RED-HEADED PINE SAWFLY DEFOLIATION ON ACCUMULATIVE ANNUAL SHORTLEAF PINE INCREMENT.



GRAPH 13. COMPARISON OF EFFECTS OF COMPLETE FIRST AND SECOND GENERATION RED-HEADED PINE SAWFLY DEFOLIATION ON ANNUAL SHORTLEAF PINE INCREMENT.



GRAPH 14. COMPARISON OF EFFECTS OF COMPLETE FIRST AND SECOND GENERATION RED-HEADED PINE SAWFLY DEFOLIATION ON ACCUMULATIVE ANNUAL SHORTLEAF PINE INCREMENT.

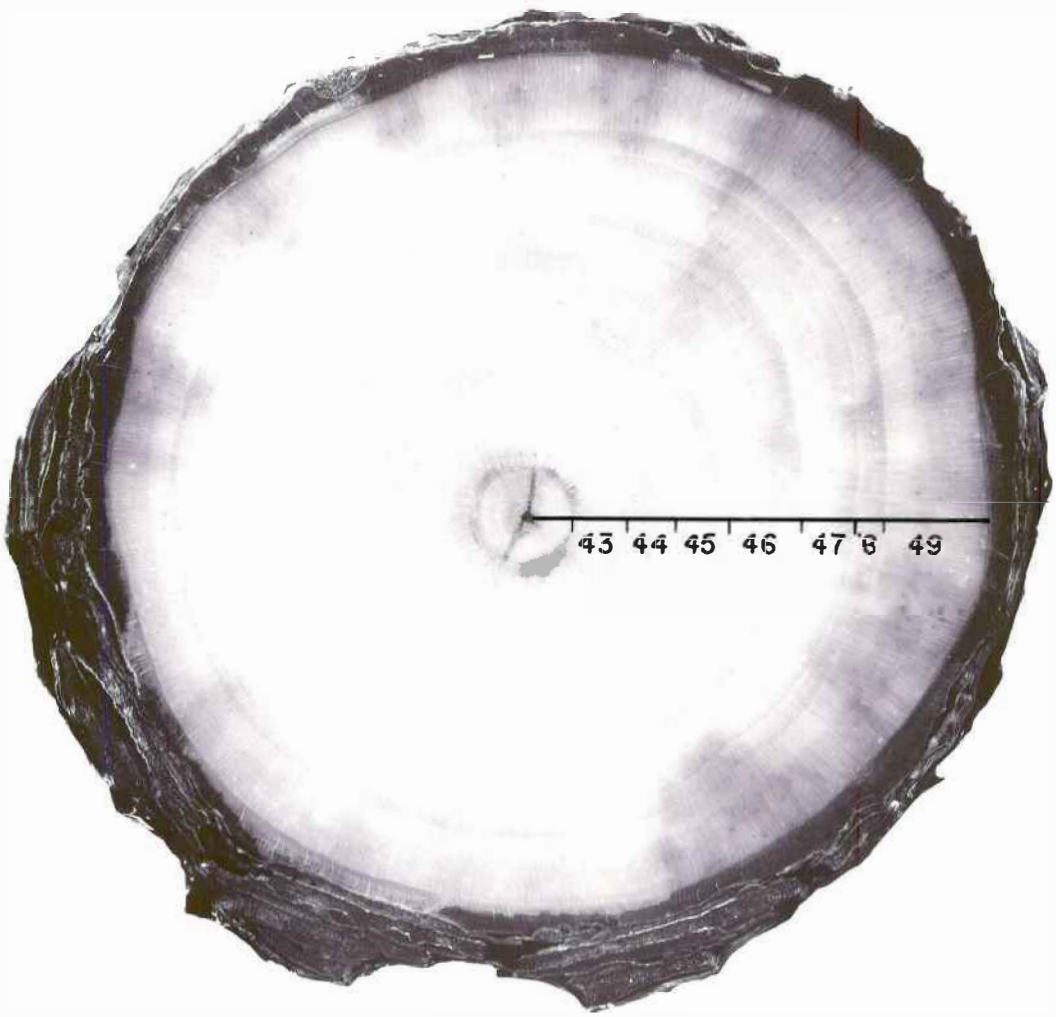


FIGURE 57. SHORTLEAF PINE ILLUSTRATING REDUCED 1948 ANNUAL RING CAUSED BY COMPLETE SECOND GENERATION 1947 RED-HEADED PINE SAWFLY DEFOLIATION.

fered a 100 percent third generation sawfly defoliation in 1946. These trees may also have been completely defoliated earlier in 1946 although no record was made of defoliation. A small square of bark and phloem was removed from the base of each tree on June 6, 1947 to wound the growing tissue so subsequent radial growth could be identified. Five trees on each plot were cut in November 1949 for radial increment studies.

The average annual radial increment of five of the foregoing trees from each plot charted on Graph 15 indicates that severe defoliation might have occurred prior to the third generation 1946 defoliation. This defoliation, combined with the third generation defoliation, caused a reduction in both the 1946 and 1947 increment. Recovery was rapid and an increase in radial growth was made in 1948 and in 1949. Graph 16 illustrates the decline in accumulated average radial increment rate caused by the severe defoliation. The growth rate on both plots was reduced slightly in 1946 and markedly so in 1947. Recovery was rapid. Figure 58 illustrates the 1947 annual ring reduction resulting from complete third generation 1946 and previous severe defoliation. The scar area indicated by the arrow was caused by removing growing tissue in early 1947. Although a difference in growth rate on the two plots appeared to exist, the recovery from severe defoliation followed the same general pattern of a reduced 1946 and 1947 increment and an increased 1948 and 1949 growth on both plots.

Five shortleaf pine trees were selected at random in the plantation in which the red-headed pine sawfly made its initial appearance in Illinois in 1945. These trees, completely stripped during the third generation in 1946, were undoubtedly stripped during either or both first and second generation in 1946. Severe defoliation was not reported subsequent to the 1946 injury.

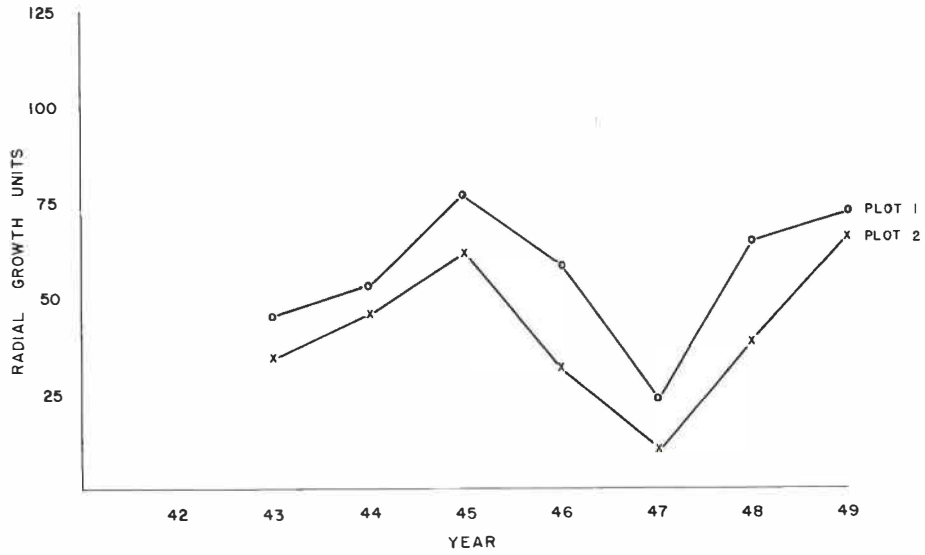
Average annual radial increment plotted in Graph 17 indicates that a severe first generation 1946 defoliation and probably second generation defoliation occurred in addition to the third generation attack. Radial growth reductions in 1946 and 1947 followed by an increase in 1948 and 1949 were similar to the pattern demonstrated in the foregoing area. Average accumulative annual increment declined in 1946 and 1947 and increased in 1948 and 1949 as experienced in the foregoing area (Graph 18).

Summary

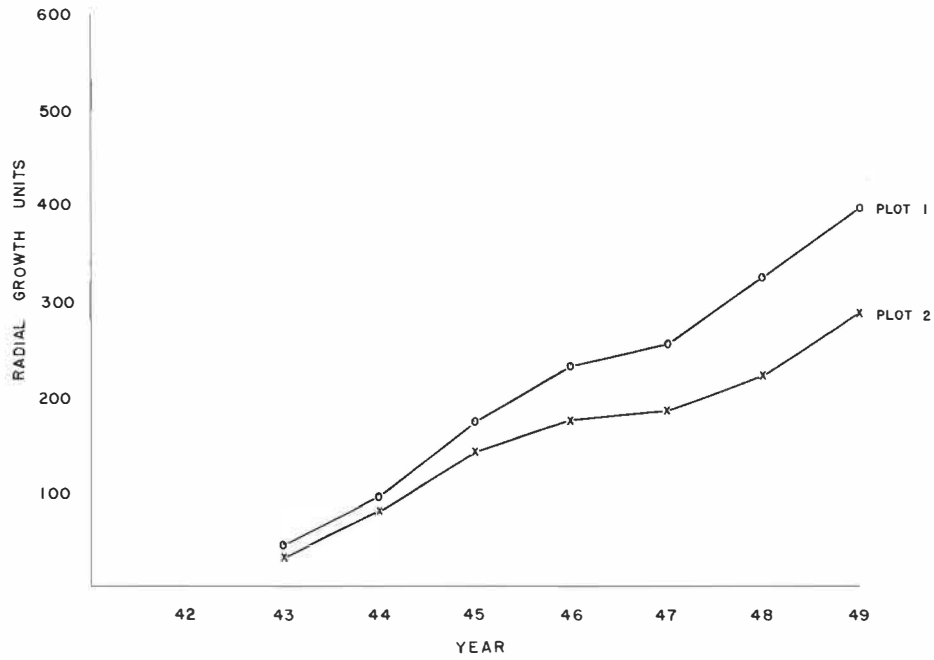
Studies of radial growth in shortleaf pine following defoliation by the red-headed pine sawfly suggests the following trends:

1. Single complete first generation defoliation caused a decline in current year's radial increment. This loss was regained through increased growth the following two years.

2. Twenty-five percent first generation defoliation caused no measurable increment loss. Fifty and 75 and 100 percent first generation defoliation caused a reduction in current radial increment in proportion to the severity of the defoliation.



GRAPH 15. EFFECT OF COMPLETE THIRD GENERATION AND PREVIOUS SEVERE RED-HEADED PINE SAWFLY DEFOLIATION ON ANNUAL SHORTLEAF PINE INCREMENT.



GRAPH 16. EFFECT OF COMPLETE THIRD GENERATION AND PREVIOUS SEVERE RED-HEADED PINE SAWFLY DEFOLIATION ON ACCUMULATIVE ANNUAL SHORTLEAF PINE INCREMENT.

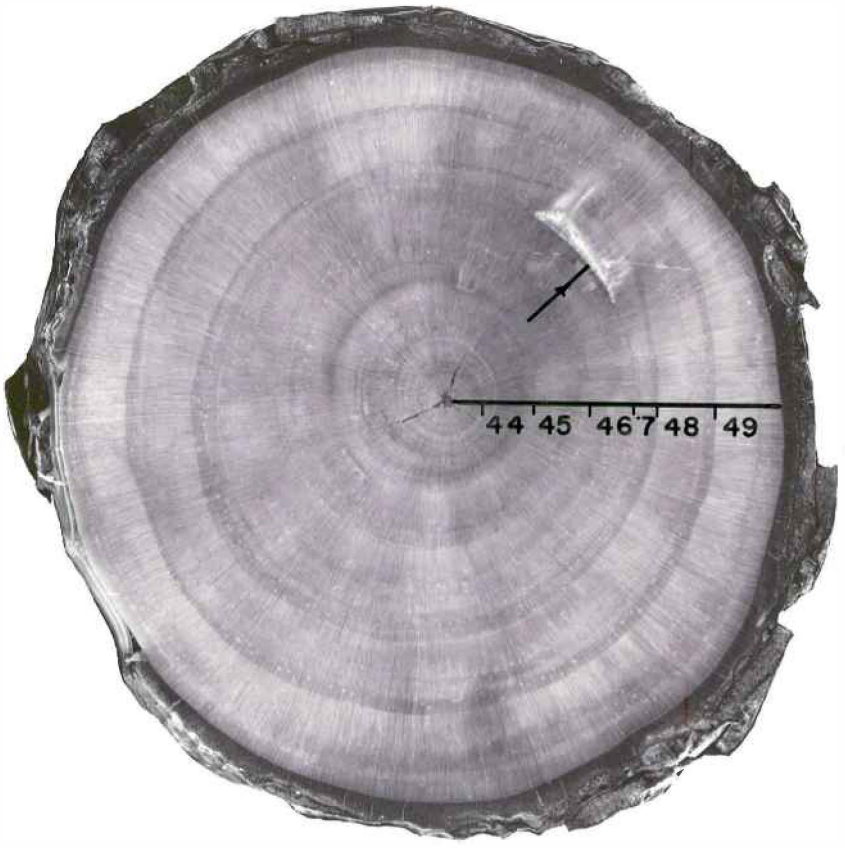
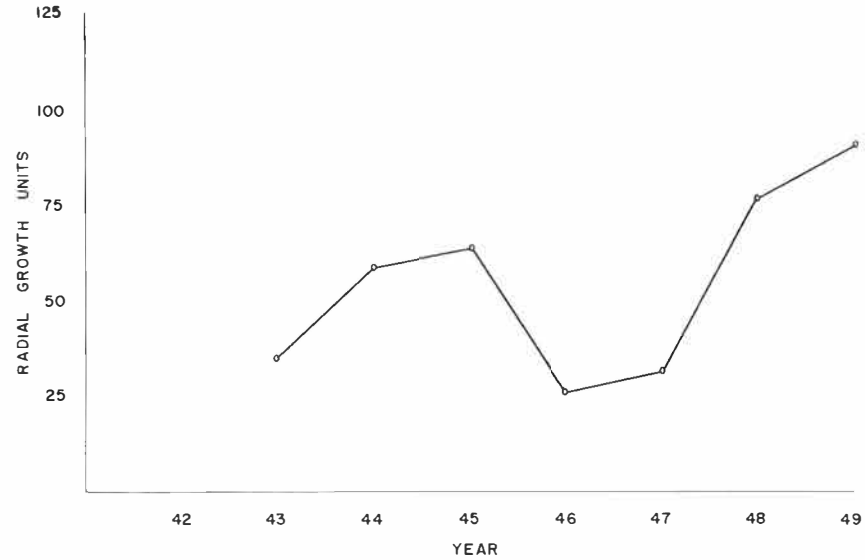
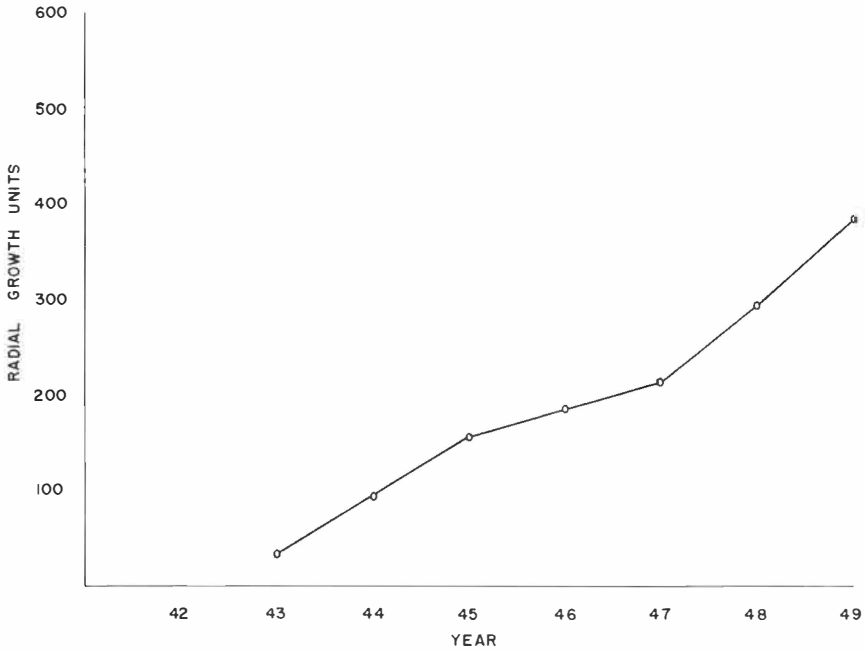


FIGURE 58. SHORTLEAF PINE ILLUSTRATING REDUCED 1947 ANNUAL RING CAUSED BY COMPLETE THIRD GENERATION AND PREVIOUS SEVERE 1946 RED-HEADED PINE SAWFLY DEFOLIATION. ARROW INDICATES SCAR AREA CAUSED BY REMOVING PHLOEM IN EARLY 1947.



GRAPH 17. EFFECT OF COMPLETE THIRD GENERATION AND PREVIOUS SEVERE RED-HEADED PINE SAWFLY DEFOLIATION ON ANNUAL SHORTLEAF PINE INCREMENT.



GRAPH 18. EFFECT OF COMPLETE THIRD GENERATION AND PREVIOUS SEVERE RED-HEADED PINE SAWFLY DEFOLIATION ON ACCUMULATIVE ANNUAL SHORTLEAF PINE INCREMENT.

3. Single complete second generation defoliation caused little decrease in the current year's increment. The effects of this defoliation were reflected in a decrease in the growth rate the year following defoliation. The increment lost was regained by increased growth during the second year following defoliation.

4. Complete third generation defoliation plus previous defoliation the same season, resulted in a decrease in growth during the current season and also during the next season. Rapid recovery was experienced during the second and third year with the growth loss being practically regained by the third year.

POPULATION SURVEY METHODS

The development of reliable sampling methods for determining relative or estimated population levels of forest insects is often difficult and is characterized by numerous complicating factors. The methods of approach differ from those used for evaluating other agricultural insect populations. Particularly is this true when the large physical size of the host plant, the acreages involved, and the value of the crop plant are considered. In addition, survey methods may be further influenced by variations in host plant composition, stand density, tree age, and shape within the forest stands. The methods are further influenced by the habits of the particular insect species and the facility with which its various life stages may be detected and examined over large forest areas. Finally, the ultimate application of the population density information will influence the method selected. Control activities, for example, may require that the method be sufficiently rapid and thorough that examination of the infested forest area can be completed before economic injury has been sustained.

Fortunately, the population problem for the red-headed pine sawfly does not present any great difficulty. The insect seldom attacks trees over 12 - 15 feet in height and generally its attack is restricted to trees in the 1-foot to 8-foot range. Also, the attack is mainly confined to plantation pines which are most often grown in uniform rows extending across the entire planted area, thus simplifying plot examination.

In population studies either the injured host or one of the insect stages may be used as a density criterion. In the following paragraphs the various survey criteria are discussed. The actual method of survey, that is the physical process and procedures, is outlined in a separate section.

Survey Criteria

Adult Stages

The feasibility of using the adult stage of the red-headed pine sawfly as a population index is somewhat questionable for a number of reasons. The individual adult sawflies are readily observed in the field but flight period is relatively short during each generation. The peak of adult emergence extends over approximately one week and the majority of the eggs are laid within 2 or at most 3 days during this period.

Studies conducted by the writer on the Shawnee National Forest during 1948 suggested that virgin female-baited traps might be used for population evaluation studies, particularly for studies at low population levels. Figure 59 illustrates the male sawfly catch of one of these traps which was hung in a plantation where sawfly adults and, later in the season, larvae were exceedingly rare. The following 1-hour catch of this trap, baited with 2 virgin females, illustrates the large number of males captured.

Time	Accumulative Male Catch
10:25 a.m.	Set
10:30 "	3
10:35 "	7
10:40 "	18
10:45 "	28
10:50 "	35
10:55 "	38
11:00 "	44
11:05 "	49
11:10 "	53
11:15 "	56
11:20 "	57
11:25 "	60
12:25 p.m.	80

The difficulties of timing trapping activities and the problem of having virgin females available during the critical period seriously restricts the use of these traps over large forest areas. Also, the attraction interference of wild females in relatively high sawfly population areas must be considered as a decided disadvantage. Possibly the best field of endeavor for using these traps lies in dispersion studies.

Neither female nor male sawflies were observed in the vicinity of lights in or around sawfly-infested pine plantations, thus ruling out light traps as a possible method of sampling. Also, the non-aggressiveness of the female sawfly and her habits of awaiting her mate precludes her from consideration in trapping activities.

Eggs

The egg stage of the red-headed pine sawfly was used as a population criterion during the early population surveys on the Shawnee National Forest in 1947. This stage proved quite satisfactory on small trees (under 4 feet) but grossly unsatisfactory when trees over 4 feet were encountered. Although the eggs were most frequently encountered on the lower, densely shaded branches on the south and east side of the open-growing trees, the examinations proved too time consuming to be of use on a forest-wide basis. The large egg parasite populations on the Shawnee National Forest, which drastically reduced sawfly hatch, practically ruled out eggs as a survey criterion on that Forest. On the northern forests, the egg parasite has not been present in large numbers and consequently has not greatly influenced the validity of this survey

FIGURE 59. MALE RED-HEADED PINE SAWFLY ADULTS ATTRACTED TO VIRGIN FEMALE BAITED TRAPS.

criterion. For a population analysis, however, egg counts, regardless of their difficulty, are most reliable. They present the best estimate of the sawfly population at the beginning of the annual cycle.

Larval Stages

From a strictly practical viewpoint, the number of larvae is the most usable population criterion. It is this stage of the insect that causes the ultimate injury and it is against this stage that control operations are directed. Once larval hatch is completed, the larvae are exposed to the rigors of their environment. Drastic population reductions, caused both by extremes of weather, as well as declinations through predation and diseases, have most certainly been encountered. Generally, however, the former are of a rather infrequent and unpredictable nature, and the latter, in the case of the red-headed pine sawfly, relatively rare.

On the Shawnee National Forest the first and early second instar larvae habitually feed well back in the sheltered, densely shaded portions of the shortleaf pine. Their small size, combined with their secretive feeding habits, somewhat limit the use of the early instars. Late in the second instar, the larvae move out into the open on the branches and leaders. It is during this stage that they are most easily observed. Their presence in exposed sites, together with the straw-like flags left as a result of their early needle edge feeding habits (Figure 13) renders them most visible. Hence, surveys begun during the late second instar are recommended.

On the northern forest areas, where slight amounts of defoliation cause injury or deformity, survey activities must begin as early as possible. Jack and red pine foliage seldom is as dense as shortleaf, the major southern host, and the early larval instars are more readily observed. Pre-control operation surveys can generally be undertaken as soon as larval hatch is completed over the forest as a whole.

Frass

Frass counts have been used successfully in population investigations of several forest insects attacking large trees. Because the red-headed pine sawfly seldom attacks trees over 12 feet to 15 feet in height, this criterion has not been employed by the writer. It was found more feasible to examine the tree for larval activity. The principle value of frass collections was in identifying previous larval feeding two or three years after injury.

Cocoons

Cocoon counts have been used with success in evaluating spruce, pine, and larch sawfly populations. Both time, as well as space, counts have proven satisfactory. Unfortunately, the cocoons of the red-headed pine sawfly are exceedingly difficult to collect in the soil. Many forest entomologists have complained about this difficulty and will readily agree that cocoon abundance as a criterion is most unsatisfactory. The last

instar larvae must migrate considerable distances before spinning their cocoons. This feature, and their migrating habits after their host has been completely stripped, presents such a wide distribution that it is impractical to search for their cocoons. In sandy soils or where a large quantity of surface debris (twigs and sticks) are present, scattered cocoons can be found with little difficulty. In loamy soil cocoon search is slightly better than futile.

Host Tree

Current or past sawfly defoliation is an excellent population evaluation criterion. It has the advantage of being visible from a distance of several feet and, on the northern forests at least, a permanency which allows examination over a several month period. Red-headed pine sawfly feeding progresses from the top of the tree and from the branch tips toward the base and the barren branches are visible from considerable distances, as illustrated in Figure 60. The straw-like flags on shortleaf pine, resulting from second instar feeding, are likewise visible from considerable distances (Figure 13). Past red-headed pine sawfly injury is probably most valuable in predicting areas which may be expected to suffer subsequent sawfly attack. Generally, as in the case of large control projects, it is necessary to predict the needs of the next season with a reasonable degree of accuracy. This often necessitates that survey activities be conducted several months in advance of the actual control project. Host injury surveys have been satisfactorily used, both on the Chequamegon and Shawnee National Forests to predict subsequent red-headed pine sawfly control needs.

Ecologically Favorable Sites

Periodic examination of plantation sites considered ecologically favorable to the sawfly will reveal the relative population status and should indicate whether an increase or decrease in the population has occurred since the last examination. The criterion employed may be either the condition of the host tree or any of the active insect stages. A list of plantation sites most favorable to sawfly attack is given earlier in this report.

Population Survey Procedures

The intensity of the population survey or the percentage of the infested area which is to be examined depends upon several factors. Of prime importance are the over-all acreages known or suspected to be infested, the severity of the outbreak, the time available, and the expenditures of time and manpower which can be devoted to the project. The purpose of the survey, i. e. whether the information is to be used in formulating control activities or for population trend studies, will also influence the intensity of the survey and the type of information to be collected. The selection of the survey criterion will depend upon the foregoing factors and on the stage of the insect or host condition during the survey period.

FIGURE 60. SHORTLEAF PINE LEADER DEFOLIATED BY RED-HEADED PINE SAWFLY LARVAE.

During the 1947 sawfly outbreak on the Shawnee National Forest pre-spray population surveys were conducted to determine the current sawfly population on the shortleaf pine plantations. The surveys were carried out under the pressure of limited time restrictions, reduced personnel, and a large infested acreage consisting of approximately 25,000 acres of widely-scattered, 20- to 350-acre plantations. In order to cover the greatest number of plantations within the allowable time, single plantations arbitrarily considered to be representative of plantation groups or blocks, were selected for examination. On each 40 acres of plantation examined, 4 strip plots of 22 trees per plot (approximately 1/50-acre per plot) were examined for current sawfly activity. The plots were located systematically at random, by taking one plot in each quarter of every 40-acre area examined. Plantations in the immediate vicinity of those included in the survey were considered to have the same degree of infestation. This method yielded satisfactory results which subsequently formed the basis for recommendations during the 3 control programs in 1947.

The purpose or objective of the population survey governs to a great extent, the type of information that is to be collected and the method to be employed. The survey procedure outlined below has proven practicable and satisfactory for estimating population levels to determine the need for the application of control measures. It is recommended that a one-quarter percent cruise be made of the infested plantations. The infestation data should be collected on a series of 10 two row plots, each 1 chain long, per 40 acres. These plots may be examined along a single line or along a series of offsets arranged as staggered steps through the plantation. The following information should be collected during the survey and assembled with a plantation map of the area:

1. Location of plantation, township, range, section and sub-section
2. Date of survey
3. Survey party
4. Percent cruise, plot location, and procedure followed
5. Rough sketch of plantation block indicating examined portions and infested area
6. Average plantation height
7. Species of pine attacked
8. Entomological information
   a. Number of infested trees (current and past) per plot
   b. Stage of insect pest - instars, etc.
   c. Rough sketch of infested area
   d. Estimate of previous and current injury

9. Outstanding topographic features - rivers, lakes, hills, telephone lines

10. Estimated amount of overstory

    a. Height

    b. Species

    c. Sky cover estimates

11. Soil type and ground cover

12. Recommendation for method of control: aerial or ground equipment

The plantation sequence to be followed during the pre-spray survey should be left to the discretion of the survey personnel. In general, it is suggested that the smaller most heavily infested areas and areas of high aesthetic value be examined early. Plantations made up primarily of the favored host located in ecologically favorable sites should also be high on the examination list.

The percentage infestation should be computed for each plantation examined. The decision concerning the advisability of applying artificial control measures should be based primarily on economic and entomological considerations outlined in the following sections.

ECONOMICS OF THE RED-HEADED PINE SAWFLY CONTROL

The ultimate decision concerning the advisability of applying insecticidal control measures to reduce red-headed pine sawfly populations must be based on sound entomological and economic considerations. This requires the close cooperation of both the foresters and entomologists. The economics are complex and too far reaching to be discussed in detail at this writing. Briefly, they should yield a rough comparison of the estimated population suppression expenditures and the likelihood of their offsetting the losses which would be sustained if no control measures were applied. Attempts to eradicate widespread native forest pests are not considered as economically sound. Also, under endemic conditions it is not generally considered economically sound to attempt further population reduction.

From the entomological standpoint population reduction can be readily accomplished through the use of one of the many recently developed organic insecticides, applied with ground or aerial equipment. This aspect of the problem will be discussed in a later section of this paper.

Shawnee National Forest

During the 1947 control program, a 10 percent infestation level in shortleaf pine plantations averaging 6 feet and less and a 20 percent infestation level in plantations averaging over 6 feet in height were

arbitrarily selected as economic damage levels. In view of the ability of shortleaf pine to recover from severe defoliation and the relatively low permanent increment loss sustained, it appears logical to delay control applications through at least one defoliation period. Decisions concerning control applications on recreational areas are left to the discretion of the forest official.

Manistee National Forest

Because of the extreme susceptibility of both jack and red pine to sawfly injury, control applications should be initiated when outbreak populations are encountered. The 10-20 percent economic damage levels outlined in the foregoing sections of this paper are recommended for use on the northern forest plantations.

CONTROL PRACTICES

The immediate and primary objective of population control practices directed against the red-headed pine sawfly on a forest-wide basis is to reduce the sawfly population below the economic damage density. The secondary objective is to reduce the sawfly population to an endemic level from which recovery to economic levels will not occur until the host trees have grown beyond the so-called susceptible age.

Timing of control applications is a critical consideration for most forest insects and the red-headed pine sawfly is no exception. Control of the sawfly may best be accomplished by destroying the larval stage during the feeding period. Attempts to destroy any of the other stages, adult, egg, or cocoon on a commercial basis will probably be unsuccessful, both from the standpoint of actual population reduction accomplished as well as from the economic standpoint. Most successful kills have been obtained on the national forest areas by delaying control spraying applications until after the majority of the larvae have passed the second instar and moved out into the more exposed feeding sites. This was particularly true on the shortleaf plantations of southern Illinois. In recent preliminary tests, however, H. C. Jacobs began residual spraying operations against the red-headed pine sawfly on the Chequamegon National Forest with DDT shortly before larval hatch began. Heavy larval mortality resulted on the two study plots and no subsequent spraying was necessary. The method shows much promise, particularly on a small tree basis.

Insecticides

A wide array of stomach poisons and contact insecticides have been tested against the red-headed pine sawfly. Since the sawfly is exceedingly susceptible to most poisons, little difficulty has been encountered in obtaining satisfactory kills with practically every poison tested. DDT appears to be the most practical insecticide for use against the sawfly from an economic standpoint. This insecticide has given excellent kills in most of its formulations. The major problem is con-

cerned with developing an efficient practical method of application which will give adequate coverage. By and large, the equipment used will dictate the formulation to be employed and the dosage to be applied. Oil solutions containing one pound of technical grade DDT per gallon of solution dispensed from aerial equipment have given satisfactory results throughout this region. Three percent DDT in oil solutions have proven satisfactory when dispensed from mist producing back-pack-type sprayers and 3 percent water suspensions of wettable DDT powder gave good kills when dispensed from hydraulic equipment.

Equipment

The selection of the most economical method of application is based on a number of factors. The size of the infested area, the length of time during which the insect is susceptible to insecticides, and the physical characteristics of the area such as the amount of hardwood overstory, accessibility, and shape will largely dictate the choice of equipment. Insecticide formulations will be determined by the type of equipment selected, as mentioned above. For aerial applications to be economically feasible, total areas in excess of approximately 500 acres must be treated. Whether this acreage can be assembled depends mainly upon the extent of the infestation, the amount of overstory covering the pine plantations, and the size of the individual plantations. Individual areas less than approximately 20 acres cannot be economically treated from the air. It is doubtful whether plantations growing under greater than 50 percent canopy can be effectively treated from the air. Control applications from the ground, using hand equipment, will be governed by the total acreage infested, the accessibility of the area, and the tree size.

Summary of Control Costs

The cost of applying control measures against the red-headed pine sawfly on national forest lands has varied somewhat throughout the North Central States. Variations in insecticide costs on the particular forests have contributed to the cost differentials, as have also the inequalities in distances to airports. Table 24 presents a summary of aerial application costs for 1946 through 1949. The final average cost per acre for the control project does not include survey or post spray evaluation costs; only aerial application flying, insecticides, labor, and transportation costs directly chargeable to the project are included. It should be pointed out that while the cost of application has decreased from a high of $1.75 per acre to an average of approximately 50¢ per acre, increased labor and insecticide costs have about offset the application gains at this time.

TABLE 24. AERIAL SPRAYING COSTS FOR RED-HEADED PINE SAWFLY CONTROL ON NATIONAL FORESTS IN REGION NINE*

Forest	Acreage Sprayed	Application Average Cost per Acre	Average Total Cost per Acre
1946			
Chequamegon	1815**	$1.00	$2.00
Manistee	710**	.30	2.55
Nicolet	1600**	?	2.22
Ottawa	220**	1.75	2.53
1947			
Chequamegon	1975*	.72	2.08
Manistee	3354*	.72	1.65
Nicolet	2450**	.71	2.32
Ottawa	1320**	.72	1.88
Shawnee - First	4596*	.97	1.80
- Second	1410*	.71	1.69
- Third	210*	.65	?
1948			
Hiawatha	480*	.60	1.71
Manistee	2240*	.55	1.52
Manistee	80**	.55	1.96
Nicolet	549*	.55	1.88
Nicolet	543**	.55	2.01
1949			
Chippewa	80***	1.20	2.27
Nicolet	119*	.56	1.41
Nicolet	1073**	.56	1.35
Ottawa	2250**	.47	2.00

* Red-headed Pine Sawfly

* Compiled from records made available by the U. S. Forest Service

** Spittlebug

*** Larch Sawfly

Table 25 presents a summary of hand or ground application costs for national forests in this region. It will be observed that many apparent discrepancies exist in the ratio of cost per acre to size of the treated area. Normally one would expect a decrease in per acre costs as the size of the project increased. Addition of equipment costs to a single project or accrediting an entire plantation to a small control project was found to bias cost account records. These results must be viewed, therefore, with some reserve and only the larger (500 to 3,000 acre) control costs considered as typical.

Two small mist blower control applications were made in 1949 for which cost data were available. On the Chequamegon National Forest 55 acres of spittlebug-infested red pine was treated at an average cost of $2.72 per acre and 30 acres of infested red pine on the Manistee National Forest was treated at $1.36 per acre.

TABLE 25. HAND SPRAYING COSTS FOR RED-HEADED PINE SAWFLY CONTROL ON NATIONAL FORESTS IN REGION NINE[a]

Forest	Acreage Sprayed	Average Total Cost per Acre
1946		
Chequamegon	300	$1.65
Hiawatha	600	2.44
Manistee	800	2.70
Shawnee	133	4.25
1947		
Chequamegon	1,593	2.02
Hiawatha	1,234	2.52
Manistee	25	15.85
Nicolet	87	0.92
Ottawa	25	0.96
1948		
Chequamegon	1,685	1.82
Chippewa	93	2.12
Hiawatha	965	4.01
Manistee	300	1.63
Nicolet	452	4.36
Shawnee	8	3.37
1949		
Chequamegon	3,708	2.30
Chippewa	95	1.88
Mark Twain	169	2.43
Nicolet	332	4.98
Ottawa	3	13.53
Shawnee	30	1.36

[a] Compiled from records made available by the U. S. Forest Service

Silvicultural Control

The possibility of reducing red-headed pine sawfly defoliation injury through silvicultural practices and planting methods lies primarily in the avoidance of situations ecologically favorable to the sawfly. In many instances, avoidance is not always possible. Susceptible sites such as sandblow areas and partially shaded sites ultimately will be planted. Also, these susceptible sites may often be unfavorable to substitute pine species which are comparatively resistant to sawfly attack. The most susceptible species of pine may thus be planted as a last resort. Under these latter conditions, artificial control measures may have to be applied to bring these susceptible plantations through their most hazardous period.

In the summary following the host-site susceptibility discussions, situations most favorable to sawfly attack were listed for the Shawnee and Manistee National Forests. Avoidance of the combinations in the upper part of the listing is strongly indicated. Obviously, it is not possible to avoid plantation edges, and plantations will be open during the first fewyears of growth.

To reduce the risk of red-headed pine sawfly attack, the following recommendations are presented. It is expected that when it is necessary to plant areas highly susceptible to sawfly attack, these plantations will be kept under surveillance and control applications undertaken if economic sawfly populations develop.

1. Shawnee National Forest

   a. Avoid planting hard pines under a hardwood overstory (Figure 45).

   b. Avoid planting within approximately one chain of all hardwood borders, or remove or girdle residual hardwoods (Figure 46).

   c. Undertake early release of plantations from weed hardwoods.

   d. Replant areas of poor survival which result in widely spaced open plantations (Figure 26).

   e. Promote early closing of plantations by close planting at no more than 6x6.

   f. Keep susceptible plantings under surveillance for sawfly population increases (Figures 26, 45).

2. Manistee National Forest

   a. Avoid planting hard pines under a hardwood overstory. This applies particularly to jack pine.

b. Avoid planting within approximately one chain of hardwood borders (Figures 27, 28).

c. Remove or girdle residual hardwoods from proposed planting site if feasible (Figures 36, 37).

d. Avoid planting within 1/2 chain of residual hardwood crowns.

e. Avoid sandblow planting where feasible (Figures 39 and 40).

f. Replant all areas of poor survival.

g. Substitute less susceptible red pine for jack pine wherever possible.

h. Keep susceptible plantations under surveillance for sawfly population increases (Figures 17, 36, 37, 39, 40, 41 and 42).

SUMMARY

Biological and ecological studies of the red-headed pine sawfly, Neodiprion leconteï (Fitch), and its control through the application of DDT sprays from aircraft were undertaken as a cooperative project between the United States Bureau of Entomology and Plant Quarantine, the United States Forest Service, and the Division of Entomology and Economic Zoology of the University of Minnesota.

The biological and ecological studies were conducted on the Shawnee National Forest in southern Illinois during 1947, 1948, and 1949, and on the Manistee National Forest in central Michigan in 1948 and 1949. Sawfly infestations on Michigan, Minnesota, Missouri, and Wisconsin national forests were also examined to round out the ecological picture. Investigations of the control of the sawfly through the aerial application of DDT sprays were conducted on the Shawnee National Forest in 1947 and on the Manistee National Forest in 1948.

The red-headed pine sawfly is considered by foresters and forest entomologists to be one of the most important native forest insects defoliating young pines in eastern North America. This sawfly confines its attack to members of the hard pine group. Since its description by Asa Fitch in 1858, the sawfly has been reported from practically every state east of the tier of states bounding the west banks of the Mississippi River from Jasper County, Texas (30° North) and Manatee County, Florida (27° North) to Kinmount, Lake, Ontario (46° North) and Alfanel, Quebec (49° North), Canada.

Outbreaks of the red-headed pine sawfly were first observed from 1922 through 1925 in New Brunswick, Canada. During the 1930's widespread outbreaks were reported in Alabama, Massachusetts, Michigan, New York, Ohio, and Tennessee. During the 1940's outbreaks in Illinois, Michigan, New York, and Wisconsin caused severe injury to young hard

pines. It was during the recent widespread outbreak that the present studies of the sawfly were undertaken.

Nine of the 10 native hard pines and 7 introduced species of pine have been recorded as hosts of the red-headed pine sawfly. In addition, migrating larvae have been observed to complete their development on two species of white pine, as well as on tamarack, cedar cedar, and Norway spruce. In the Lake States, studies indicate that the sawfly prefers jack pine. Red, Scotch, Austrian, and mugho pines are also attacked, but less frequently. The preference for jack pine is often reflected in the complete defoliation of this species before other nearby hard pine species are attacked. In one plantation where a solid block of jack pine met a solid block of red pine, the preference was for jack pine, both from the standpoint of number of trees attacked as well as from the standpoint of number of colonies of sawflies per tree. For example, all of the first row jack pines were attacked as compared to 33 percent of the first row red pines; the first row of jack pines averaged 6.5 sawfly colonies per tree as compared to an average of 1.5 sawfly colonies per attacked red pine.

In the southern part of the United States, shortleaf pine is the preferred host. South of the range of shortleaf pine, loblolly, longleaf, and slash pines are attacked. In the northeastern part of the United States, red and jack pine are preferred, while in Canada, red pine is selected. In all regions within the range of the sawfly the available species of hard pine is attacked in the absence of the preferred host.

The red-headed pine sawfly overwinters as a prepupa in a cocoon spun in the soil in the vicinity of the infested host. With the onset of warm weather in spring, pupation occurs. Emergence of the adults, mating, and oviposition soon follow. The females deposit an average of 102 to 141 eggs per batch in a series of shoe-shaped pockets cut in the pine needle. The number of eggs per needle varies with the host species from an average of 5.6 eggs per Virginia pine needle to 12.2 eggs per red pine needle. Practically the entire complement of eggs is laid by the female. An average of from 2 to 3 eggs were dissected from females following the completion of oviposition.

The progeny of each female sawfly feed as a gregarious colony throughout their larval period. The newly hatched sawfly larvae chew cup-shaped notches in the needles in which the oviposition occurred. During the second instar, the larvae feed on the mesodermal parts of the pine needles and leave the central vascular tissue as straw-like flags. Beginning with the third instar, the colony moves out into the open to feed on the leader and branch tip needles. Defoliation progresses from the top of the tree toward the base during the fourth and fifth instars. Larvae readily leave completely defoliated hard pines and migrate up to 19 feet across bare sand to establish themselves on nearby pines. In many instances the migrating larvae cause severe defoliation of these new hosts. Heavy mortality among migrating larvae occurred when they encountered soil surface temperatures above 105° F. Migration across sodded areas was more successful as the larvae could escape high

soil surface temperatures by climbing blades of grass. From 3 to 5 generations of the sawfly per year have been reported in southern United States, 2 to 3 generations per year in the mid-central areas, and 1 generation per year in the northern sections and in Canada. Diapause up to 5 years duration has been reported.

Fifty-eight species of parasites and predators were reported attacking the sawfly. Twenty-one were collected exclusively in the United States, 23 exclusively in Canada, and 14 in both the United States and Canada. Studies conducted on the Shawnee National Forest in 1947 and 1948 indicated that the egg parasite, Closterocerus cinctipennis Ashm., was a prime factor in reducing the sawfly population. Parasitism varied from 6.1 percent to 100 percent. In one pitch pine plantation, parasitism averaged 95.2 percent over a 2-1/2 year period. Among the larval parasites, Spathiusgenia spinigera Ths. and Phorocera humata A. & W. were the most important on the Shawnee National Forest.

In ecological studies of high populations on the Shawnee National Forest it was found that a linear relationship existed between the number of trees infested and the degree of defoliation of the attacked trees. On shortleaf pine plantations ranging from 4.0 to 6.9 feet in height defoliation injury increased from 28 percent at the 10 percent infestation level to 58 percent at the 75 percent infestation level. On plantations ranging from 2.0 to 3.9 feet, 33 percent defoliation was sustained at the 10 percent infestation level and 73 percent defoliation at the 75 percent infestation level. Practical application of these data can be made in predicting sawfly defoliation intensities at various infestation levels in shortleaf pine plantations.

On the Manistee National Forest preliminary studies indicate a linear relationship between the intensity of the infestation and the number of sawfly colonies per jack pine tree. As the percent infestation increased greater numbers of trees suffered multiple attack. For instance, at the 10 percent infestation level, an average of 1 colony per tree was encountered. At the 60 percent infestation level, an average of 2 colonies per tree were encountered.

Studies of the rate of defoliation by 1, 2, 4, and 8 colonies per tree for four height classes of jack and red pine were undertaken to determine the rate and intensity of defoliation, and also the migrating habits of the sawfly. Although disease killed many of the larvae before defoliation was completed, general trends indicate that the amount of injury was influenced by both time and population concentration limitations.

Site preference studies in epidemic areas revealed that shaded plantations suffered most severely from sawfly attack. Defoliation on the Shawnee National Forest was more severe and the number of trees attacked greater in the shaded areas than in the open areas. Oviposition by female sawflies was concentrated in the shaded portions of pine plantations and on the shaded portions of open-growing pines. The same situation was found on the Manistee National Forest. Heavy attacks were most

common on 1) the edges of pine plantations shaded by bordering hardwoods, 2) pine plantations shaded by single residual hardwoods within the stand, 3) sandblow plantations, and 4) non-closed, poor survival plantations. In most instances sawfly egg concentrations were observed in the shaded parts of the pines. From a survey of 560 acres of jack pine plantation it was apparent that a linear relationship existed between the amount of hardwood cover and the number of trees attacked by the sawfly.

Low population studies on the Shawnee National Forest indicate that reservoir populations are being maintained on the shaded pines and on poor survival areas during the endemic phase of the sawfly gradation. On the Manistee National Forest reservoir populations are also being maintained on the shaded pines and on the sandblow and poor survival areas. In several instances, reproduction coming in under hardwoods shading previously killed jack pine was heavily attacked by the sawfly.

Of the various meteorological factors that affect the red-headed pine sawfly, light seemed to be of prime importance in determining the oviposition site. Studies of shadow patterns cast by single hardwoods in areas of heavy sawfly attack showed a close agreement between the 10:00 a.m., 12:00 m., and 2:00 p.m. hardwood shadow cast during the oviposition period and the area of complete sawfly defoliation. The length of growing season is closely correlated with the number of generations per year of the sawfly in the United States. A map of predicted number of generations per year based on frost free days and number of generations per year of the sawfly reported in the field is presented.

The ability of the host to withstand sawfly defoliation varies according to the tree species attacked. In the northern part of the United States and Canada, jack and red pines succumb to a single complete defoliation. Single branches normally die when they are completely stripped of their foliage. Incompletely defoliated branches frequently survive when a few needles or partially consumed needles remain. Several of the southern hard pines have been reported able to withstand complete defoliation. To determine the effects of varying degrees of sawfly defoliation of shortleaf pine, 125 trees were tagged on the Shawnee National Forest in 1947. In November 1949 these trees were re-examined for mortality, vigor, and height growth. Several trees in each defoliation category were cut for annual increment determinations.

All shortleaf pines survived defoliation intensities up to 100 percent resulting from first and second generation sawfly feeding. Only 7 percent of the trees succumbed following complete third generation sawfly defoliation (1946) and possibly previous severe attack. Height growth was good on all trees but heavy injury resulting from Nantucket pine moth infestations may have masked differences in height growth caused by sawfly defoliation. Differences in radial growth reflected the influence of partial and complete defoliation. First generation defoliation effects below 50 percent were not evident. Defoliation of 50, 75, and 100 percent caused increasingly greater immediate reduction in annual increment. These losses were temporary and the trees recovered their losses with an increased annual increment

the following two years. Complete second generation defoliation caused no immediate radial increment reduction as the pines had about completed their growth by the time defoliation occurred. This defoliation was reflected in a reduced annual increment the next year. The increment loss was regained during the second year following defoliation. Complete third generation sawfly defoliation preceded by previous severe defoliation was reflected in a decreased annual increment the following year. Increased increment the next two years compensated for the losses.

For surveys several criteria may be used. The use of frass or the adult, egg, and cocoon stages is not recommended due to the difficulties encountered in observing them in the field. The larval stages and the presence or absence of host injury show the most promise.

Control of the red-headed pine sawfly larvae is readily accomplished using either ground or aerial equipment to dispense insecticides. DDT has thus far proven to be the most practical insecticide to use with either type of equipment. For aerial applications oil solutions containing 1 pound of DDT per gallon have been satisfactory. Three percent oil solutions are recommended for use with hand equipment. A summary of application costs for the past 4 seasons indicates that current aerial applications ranged from $1.25 to $2.25 per acre and ground applications from $2.30 to $5.00 per acre depending upon the acreages involved.

The possibility of reducing red-headed pine sawfly populations through silvicultural practices is discussed. The planting of sites ecologically favorable to sawfly attack should be avoided. If these areas must be planted, it is recommended that they be kept under surveillance for evidence of injury.

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